A TEXT-BOOK OF ZOOLOGY

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PREFACE TO THE FIRST EDITION

In spite of its bulk, the present work is strictly adapted to the needs of the beginner. The mode of treatment of the subject is such that no previous knowledge of Zoology is assumed, and students of the first and second years should have no more difficulty in following the accounts of the various groups than is incidental to the first study of a complex and unfamiliar subject.

There can be little doubt that the study of Zoology is most profitably as well as most pleasantly begun in the field and by the sea-shore, in the Zoological Garden and the Aquarium. In a very real sense it is true that the best zoologist is he who knows the most animals, and there can certainly be no better foundation for a strict and scientific study of the subject than a familiarity with the general appearance and habits of the common members of the principal animal classes. But Zoology as a branch of academical study can hardly be pursued on the broad lines of general natural history, and must be content to lose a little in breadth of view—at least in its earlier stages—while insisting upon accurate observation, comparison, and induction, within the limited field of Laboratory and Museum work.

A not uncommon method of expounding the science of Zoology is to begin the study of a given group by a definition, the very terms of which it is impossible that the student should understand; then to take a general survey of the group, illustrated by casual references to animals and to structures of which it is highly unlikely he has ever heard; and, finally, to descend to a survey of the more important forms included in the group. It will probably be generally agreed that, from the teacher's point of view, this method begins at the wrong end, and is hardly more rational than it would be to deliver a course on the general characteristics of English Literature, suitably illustrated by "elegant extracts," to a class of students who had never read a single English poet or essayist.

There can be no question as to the vast improvement effected in zoological teaching by the practice of preceding the study of a given group as a whole by the accurate examination of a suitable member of it. With the clear mental image of a particular animal, in the totality of its organization, the comparison of the parts and organs of other animals of like build becomes a profitable study, and the danger of the comparative method—that the student may learn a great deal of the systems of organs in a group without getting a clear conception of a single animal belonging to it—is much diminished.

The method of "types" has, however, its own dangers. Students are, in

their way, great generalizers, and, unless carefully looked after, are quite sure to take the type for the class, and to consider all Arthropods but crayfishes and cockroaches, and all Molluscs but mussels and snails, as non-typical. For this reason a course of Zoology which confines itself entirely or largely to " types," or, as we prefer to call them,[1] examples, is certain to be a singularly narrow and barren affair, and to leave the student with the vaguest and most erroneous ideas of the animal kingdom as a whole. This is especially the case when the number of examples is small, each of the Phyla being represented by only one or two forms.

In our opinion every group which cannot readily and intelligibly be described in terms of some other group should be represented, in an elementary course of Zoology, by an example. We have, therefore, in the majority of cases, described, in some detail, an example of every important class, and, in cases where the diversity of organization is very great—as in Crustacea and Fishes—two or more examples are taken. The student is thus furnished with a brief account of at least one member—usually readily accessible—of all the principal groups of animals.

By the time the example has been studied, a definition of the class and of its orders will convey some idea to the mind, and will serve to show which of the characters already met with are of distinctive importance, and which special to the example itself. In order to bring out this point more clearly, to furnish a connection between the account of the example and that of the class as a whole, and to give some idea of the meaning of specific, generic, and family characters, we have introduced, after the classification, a paragraph giving the systematic position of the example, sometimes in more, sometimes in less detail.

Following the table of classification with its brief definitions comes the general account of the group. This is usually treated according to the comparative method, the leading modifications of the various parts and organs being described *seriatim*. In a few cases this plan has been abandoned and the class described order by order, but this is done only when the deviations from the type are so considerable as to lead us to think the comparative method unsuitable for beginners. On the other hand, when all the classes of the phylum present a very uniform type of structure, the phylum is studied comparatively as a whole. The description of each group usually ends with some account of its ethology and distribution, and with a discussion of its affinities and of the mutual relationships of its various subdivisions.

We have done our best to make the space devoted to each group proportional to its complexity and range of variation, and to subdue the natural tendency to devote most attention to the more recently investigated classes, or to those in

[1] Following a suggestion for which we are indebted to Dr. Alexander Hill, Master of Downing College, Cambridge.

which we ourselves happen to be especially interested. A few lesser groups have been put into small type, partly to economize space, partly because they seem to us to be of minor importance to the beginner.

Following out the plan of deferring the discussion of general questions until the facts with which they are connected have been brought forward, we have placed the sections on Distribution, on the Philosophy of Zoology, and on the History of Zoology at the end of the book. We have, however, placed a general account of the structure and physiology of animals immediately after the Introduction, and one on the Craniate Vertebrata before the description of the classes of that division, but it will be obvious that these deviations from the strictly inductive method were inevitable in order to avoid much needless repetition.

After a good deal of consideration we have decided to omit all references to the literature of the subject in the body of the work. Anything like consistent historical treatment would be out of place in an elementary book; and the introduction of casual references to particular discoveries, while they might interest the more advanced reader by giving a kind of personal colouring to the subject, could hardly fail, from their necessarily limited character, to be misleading to the beginner, and to increase rather than diminish his difficulties. We have, therefore, postponed all reference to the history of the science to the concluding Section, in which the main lines of progress are set forth, and have given, as an Appendix, a guide to the modern literature of Zoology. The latter is intended merely to indicate the next step to be taken by the student who wishes to acquire something more than a mere text-book knowledge.[1]

The various Sections have been written by the authors in fairly equal proportions, but the work of each has been carefully read and criticized by the other, and no disputed point has been allowed to stand without thorough discussion. We are therefore jointly and severally responsible for the whole work.

A very large proportion of the figures have been specially drawn and engraved for the book. Those in which no source is named are from our own drawings, with the exception of Figs. 571, 572, 1017, 1018, 1019, 1022, 1059, 1063, and 1071, for which we are indebted to Mrs. W. A. Haswell. Figs. 1002 *bis*, 1005 *bis*, are from photographs kindly taken for us by Mr. A. Hamilton.[2]

[1] In this connection we cannot resist the pleasure of quoting two passages, exactly expressing our own views, from the preface to Dr. Waller's *Human Physiology*, which came under our notice after the above paragraph was in type: "I have given a Bibliography after some hesitation, feeling that references to original papers are of no use to junior students, and must be too imperfect to be satisfactory to more advanced students. . . . Attention has been paid to recent work, but I have felt that the gradually-formed deposit of accepted knowledge must be of greater intrinsic value than the latest 'discovery' or of the newest theory. An early mental diet in which these items are predominant is an unwholesome diet; their function in elementary instruction is that of condiments, valuable only in conjunction with a foundation of solid food."

[2] The figures referred to are numbered 618, 619, 1091, 1092, 1093, 1096, 1140, 1144, 1152, 1074, and 1078 in the 3rd edition.

Many blocks have been borrowed from well-known works, to the authors and publishers of which we beg to return our sincere acknowledgements. All the new figures have been drawn by Mr. M. P. Parker.

We have received generous assistance from Professors Arthur Dendy, G. B. Howes, Baldwin Spencer, and J. T. Wilson, and from Mr. J. P. Hill and Dr. Arthur Willey. Professor W. N. Parker has very kindly read the whole of the proof-sheets and favoured us with many valuable suggestions, besides acting as referee in numerous minor difficulties which would otherwise have cost a delay of many weeks.

It is a mere truism to say that a text-book can never really reflect the existing state of the science of which it treats, but must necessarily be to some extent out of date at the time of publication. In the present instance, the revises of the earlier pages, giving the last opportunity for any but minor alterations, were corrected in the latter part of 1895, and the sheets passed for press in the middle of 1896. We are, therefore, fully alive to the fact that much of our work already needs a thorough revision, and can console ourselves only by reflecting that " to travel hopefully is a better thing than to arrive, and the true success is to labour."

We may mention, in conclusion, that, whatever may be the merits or demerits of the book, it enjoys the distinction of being unique in one respect. The two authors have been separated from one another, during the greater part of their collaboration, by a distance of 1200 miles, and the manuscript, proofs, and drawings have had to traverse half the circumference of the globe in their journeys between the authors on the one hand, and the publishers, printers, artist, and engravers on the other. It will, therefore, be readily believed that all persons concerned have had every opportunity, during the progress of the work, of exercising the supreme virtue of patience.

PREFACE TO THE SIXTH EDITION

WHEN the preparation of a new edition of this work was planned, it was clear that this had to be based on a thorough revision of both text and illustrations. In the nineteen years that have passed since Prof. W. A. Haswell revised the text of this volume for the third edition, our ideas concerning general aspects of phylogeny and details of classification have undergone changes which cannot any longer be ignored in a text-book of this kind.

As is well known, " Parker and Haswell " represents an attempt at an *inductive* treatment of the subject matter, based on detailed type descriptions to which in every case are added an account of the classification and an extensive comparative account of the general organization of the members of the group. It has been my aim to preserve the fundamental plan and character of the book. Numerous more or less extensive alterations and emendations have been made in all sections of this volume, and it was attempted to insert them with as little incongruity in the mode of presentation as possible. The major changes may be enumerated as follows :

The chapter on the " General Structure and Physiology of Animals " has been largely rewritten and nearly all the illustrations are new. The original scope of this chapter, however, has not been considerably widened, the sole aim of this general outline being to provide the student with what may be called a comprehensive glossary of fundamental morphological and physiological terms, which, in later parts of the book, are used without further explanation.

The hypothetical phyla Nemathelminthes, Trochelminthes, and Molluscoida have been abandoned and their former members, whose affinities are more or less uncertain, are now loosely assembled in two separate sections. The section containing the non-cœlomate Nematoda, Nematomorpha, Acanthocephala, Rotifera, and Calyssozoa (Endoprocta) follows the description of the Platyhelminthes, and the section containing the cœlomate Bryozoa (Ectoprocta), Phoronida, Brachiopoda, and Chætognatha precedes the description of the Echinodermata. The latter are now included in the last section of this volume. All chapters dealing with classification have been thoroughly revised and the examples included will enable the student to ascertain the systematic position of the animals mentioned in the comparative chapters on " General Organization." The paragraphs headed " Distinctive Characters," which represent short summaries of the most important group characters, have now been contrasted against the rest of the text by the use of special type.

Of the 733 text-figures contained in the present edition, 82 are replacements

of discarded illustrations and 70 are new to the volume altogether. Besides, smaller alterations have been made to a number of old text-figures. All diagrammatic representations of phylogenetic relationships have been omitted in this volume. They were in most cases out of date, and it was felt that they could not have been replaced by similar diagrams without overburdening the text with additional theoretical discussions of phylogenetic problems.

For the permission to reproduce illustrations acknowledgement is due to: Edward Arnold (" An Introduction to the Study of the Protozoa," Minchin); Messrs. Baillière, Tindall & Cox (" The Biology of the Protozoa," Calkins); Messrs. A. & C. Black (" Treatise on Zoology," Lankester); Cambridge University Press (" Zoology," Shipley & MacBride; " The Invertebrata," Borradaile, Eastham, Potts & Saunders); Verlag Gustav Fischer (" Lehrbuch der Entomologie," Weber; " Lehrbuch, der Protozoenkunde," Doflein-Reichenow); Verlag Walter de Gruyter & Co. (Kükenthal's " Handbuch der Zoologie "); Verlag Klinkhardt (" Die Strudelwürmer," Steinmann-Bresslau); Messrs. H. K. Lewis & Co., Ltd. (" Comparative Anatomy," Neal & Rand); Liverpool University Press (" Asterias," Chadwick; " Sagitta," Burfield); The Macmillan Company (" The Cell in Development and Heredity," Wilson; " Animal Biology," Woodruff); Macmillan & Co., Ltd. (" Text-book of Embryology," MacBride; " The Cambridge Natural History "; " Zoology for Medical Students," Graham Kerr); McGraw-Hill Book Company, Inc. (" Protoplasm," Seifriz); Messrs. Methuen & Co., Ltd. (" Text-book of Entomology," Imms); Oxford University Press (" Manual of Zoology," Borradaile); Verlag Julius Springer (" Lehrbuch der Zoologie," Claus, Grobben & Kühn); Verlag Georg Thieme (" Grundriss der Allgemeinen Zoologie," Kühn).

OTTO LOWENSTEIN.

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OF UNCERTAIN AFFINITIES.

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,, 4. DENDROCHIROTÆ.
,, 5. MOLPADIDA.
,, 6. SYNAPTIDA.

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,, III. **BLASTOIDEA.**
,, IV. **EDRIASTEROIDEA.**

ZOOLOGY

INTRODUCTION

Zoology, the branch of Natural History which deals with animals, is one of the two subdivisions of the great science **Biology,** which takes cognisance of all *organisms,* or things having life, as distinguished from such lifeless natural objects as rocks and minerals. The second of the two subdivisions of biology is **Botany,** which deals with plants.

The subject-matter of zoology, then, is furnished by the animals which inhabit the land-surface, the air, and the salt and fresh waters of the globe: the aim of the science is to find out all that can be known of these animals, their structure, their habits, their mutual relationships, their origin.

The first step in the study of zoology is the recognition of the obvious fact that the innumerable individual animals known to us may be grouped into what are called **species,** the members of which resemble one another so closely that to know one is to know all. The following example may serve to give the reader a fairly accurate notion of what zoologists understand by species, and of the method of naming species which has been in use since the time of the great Swedish naturalist Linnæus.

The Domestic Cat, the European Wild Cat, the Ocelot, the Leopard, the Tiger, and the Lion are animals which agree with one another in the general features of their organisation—in the number and form of their bones and teeth, in the possession of retractile claws, and in the position and characters of their internal organs. No one can fail to see that these animals, in spite of differences of size, colour, markings, etc., are all, in the broad sense of the word, "Cats." This is expressed in the language of systematic zoology by saying that they are so many **species** of a single **genus**.

According to the system of *binomial nomenclature* introduced by Linnæus, each kind of animal receives two names—one the *generic name,* common to all species of the genus; the other the *specific name,* peculiar to the species in question. Both generic and specific names are Latin in form, and are commonly Latin or Greek in origin, although frequently modern names of persons or places, with latinized terminations, are employed. In giving the name of an animal, the generic name is always placed first, and is written with a capital letter, the specific name following it, and being written, as a rule, with a small letter. For instance, to take the examples already referred to, the Domestic Cat is called *Felis domestica,* the European Wild Cat *F. catus,* the Leopard *F. pardus,* the Tiger *F. tigris,* the Lion *F. leo.* Thus the systematic name of an animal is

something more than a mere appellation, since it indicates the affinity of the species with other members of the same genus: to name an animal is, in fact, to classify it.

It is a matter of common observation that no two individuals of a species are ever exactly alike: two tabby cats, for instance, however they may resemble one another in the general characters of their colour and markings, invariably present differences in detail by which they can be readily distinguished. *Individual variations* of this kind are of universal occurrence. Moreover, it often happens that the members of a species are divisible into groups distinguishable by fairly constant characters: among Domestic Cats, for instance, we find white, black, tabby, grey, and tortoiseshell cats, besides the large long-haired Persian breed, and the tailless Manx Cat. All these are distinguished as *varieties* of the single species *Felis domestica*.

It is often difficult to decide whether two kinds of animals should be considered as distinct species or as varieties of a single species, and no universal rule can be given for determining this point. Among the higher animals mutual fertility is a fair practical test, the varieties of a species usually breeding freely with one another and producing fertile offspring, while distinct species either do not breed together or produce infertile *hybrids* or mules. Compare, for instance, the fertile mongrels produced by the union of the various breeds of Domestic Dog with the infertile mule produced by the union of the Horse and Ass. But this rule is not without exception, and in the case of wild animals is, more often than not, impossible of application: failing it, the only criterion of a "good species" is usually the presence of constant differences from allied species. Suppose, for instance, that a naturalist receives for description a number of skins of wild cats, and finds, after an accurate examination, that in some specimens the tail is two-thirds the length of the body and the skin of a uniform reddish tint with a few markings on the head, while in the rest the tail is nearly half as long as the body, and the skin tawny with black stripes. If there are no intermediate gradations between these two sets of individuals, they will be placed without hesitation in distinct species: if, on the other hand, there is a complete series of gradations between them, they will be considered to form a single variable species.

As, therefore, animals have to be distinguished from one another largely by structural characters, it is evident that the foundations of a scientific zoology must be laid in **Morphology,** the branch of science which deals with form and structure. Morphology may be said to begin with an accurate examination of the external characters; the divisions of the body, the number and position of the limbs, the characters of the skin, the position and relations of the mouth, eyes, ears, and other important structures. Next the internal structure has to be studied, the precise form, position, etc., of the various organs, such as brain, heart, and stomach, being made out: this branch of morphology is distinguished

as **Anatomy.** And, lastly, the various parts must be examined by the aid of the microscope, and their minute structure, or **Histology,** accurately determined. It is only when we have a fairly comprehensive knowledge of these three aspects of a given animal—its external characters, its rough anatomy, and its histology —that we can with some degree of safety assign it to its proper position among its fellows.

An accurate knowledge of the structure of an animal in its adult condition is not, however, all-sufficient. Nothing has been made more abundantly clear by the researches of the last half-century than that the results of anatomy and histology must be checked, and if necessary corrected, by **Embryology**—*i.e.*, by the study of the changes undergone by animals in their development from the egg to the adult condition. A striking instance is afforded by the common Barnacles which grow in great numbers on ships' bottoms, piers, etc. The older zoologists, such as *Linnæus*, grouped these creatures, along with Snails, Mussels, and the like, in the group Mollusca, and even the great anatomical skill of *Cuvier* failed to show their true position, which was made out only when *Vaughan Thompson* proved, from a study of the newly hatched young, that their proper place is among the Crustacea, in company with Crabs, Shrimps, and Water-fleas.

Given a sound knowledge of the anatomy, histology, and embryology of animals, their **Classification** may be attempted—that is, we may proceed to arrange them in groups and sub-groups, each capable of accurate definition.

The general method of classification employed by zoologists is that introduced by *Linnæus*, and may be illustrated by reference to the group of Cats which we have already used in the explanation of the terms genus, species, and variety.

We have seen that the various kinds of true Cat—Domestic Cat, Lion, Tiger, etc.—together constitute the genus *Felis*. Now, there is one member of the cat-tribe, the Cheetah, or Hunting Leopard, which differs from all its allies in having imperfectly retractile claws and certain peculiarities in its teeth. It is therefore placed in a distinct genus, *Cynælurus*, to mark the fact that the differences separating it from any species of Felis are of a more fundamental character than those separating the species of Felis from one another.

The nearest allies of the Cats are the Hyænas, but the presence of additional teeth and of non-retactile claws—to mention only two points—makes the interval between Hyænas and the two genera of Cats far greater than that between Felis and Cynælurus. The varying degree of difference is expressed in classification by placing the Hyænas in a separate **family,** the *Hyænidæ*, while Felis and Cynælurus are placed together in the family *Felidæ*. Similarly, the Civets and Mongooses form the family *Viverridæ;* the Dogs, Wolves, Jackals, Foxes, etc., the family *Canidæ;* Bears, the family *Ursidæ;* and so on.

All the foregoing animals have sharp teeth adapted to a flesh diet, and their toes are armed with claws. They therefore differ fundamentally from such animals as Sheep, Deer, Pigs, and Horses, which have flat teeth adapted for

grinding vegetable foods, and hoofed feet. The differences here are obviously far greater than those between any two of the families mentioned above, and are emphasized by placing the flesh-eaters in the **order** *Carnivora*, the hoofed animals in the order *Ungulata*. In the same way gnawing animals, such as Rats, Mice, and Beavers, form the order *Rodentia;* pouched animals, such as Kangaroos and Opossums, the order *Marsupialia;* and so on.

Carnivora, Ungulata, Rodentia, Marsupialia, etc., although differing from one another in many important respects, agree in the possession of a hairy skin and in the fact that they all suckle their young. They thus differ from Birds, which have a covering of feathers and hatch their young from eggs. The differences here are considerably more important than those between the orders of quadrupeds referred to, and are expressed by placing the latter in the **class** *Mammalia*, while Birds constitute the class *Aves*. In the same way the scaly, cold-blooded Lizards, Snakes, Tortoises, etc., form the class *Reptilia;* the slimy-skinned, scaleless Frogs, Toads, and Salamanders the class *Amphibia;* and the finned, water-breathing Fishes the class *Pisces*.

Mammals, Birds, Reptiles, Amphibians, and Fishes all agree with one another in the possession of an internal skeleton—an important part of which is an axial rod or vertebral column—and in never having more than two pairs of limbs. They thus differ in some of the most fundamental features of their organization from such animals as Crabs, Insects, Scorpions, and Centipedes, which have a jointed external skeleton, and numerous limbs. These differences—far greater than those between classes—are expressed by placing the backboned animals in the **phylum** *Chordata*, the many-legged armoured forms in the phylum *Arthropoda*. Similarly, soft-bodied animals with shells, such as Oysters and Snails, form the phylum *Mollusca*, Polypes and Jelly-fishes the phylum *Cœlenterata*. And finally the various phyla recognized by zoologists together constitute the **kingdom** *Animalia*.

Thus the animal kingdom is divided into phyla, the phyla into classes, the classes into orders, the orders into families, the families into genera, and the genera into species, while the species themselves are assemblages of individual animals agreeing with one another in certain constant characters. It will be seen that the *individual* is the only term in the series which has a real existence; all the others are mere groups formed, more or less arbitrarily, by man.

To return to the animal originally selected as an example, it will be seen that the zoological position of the Domestic Cat is expressed as follows :—

Kingdom—ANIMALIA.
 Phylum—CHORDATA.
  Class—MAMMALIA.
   Order—CARNIVORA.
    Family—*Felidæ*.
     Genus—*Felis*.
      Species—*F. domestica*.

The object of systematic zoologists has always been to find a *natural* as opposed to an *artificial* classification of animals. Good instances of artificial classification are the grouping of Bats with Birds on the ground that they both possess wings, and of Whales with Fishes on the ground that they both possess fins and live in the water. An equally good example of a natural classification is the grouping of both Bats and Whales under the head of Mammalia because of their agreement, in all essential points of anatomy, histology, and embryology, with the hairy quadrupeds which form the bulk of that class.

With the older zoologists the difficulty was to find some general principle to guide them in their arrangement of animals—some true criterion of classification. It was believed by all but a few advanced thinkers that the individuals of each species of animal were descended from a common ancestor, but that the original progenitor of each species was totally unconnected with that of every other, having, as *Buffon* puts it, "participated in the grace of a distinct act of creation."

The point of view underwent a complete change when, after the publication of Darwin's *Origin of Species* in 1859, the **Doctrine of Descent** or of **Organic Evolution** came to be generally accepted by biologists. A species is now looked upon, not as an independent creation, but as having been derived by a natural process of descent from some pre-existing species, just as the various breeds of Domestic Fowl are descended from the little Jungle-fowl of India. On this view the resemblances between species referred to above are actually matters of relationship, and species are truly allied to one another in varying degrees since they are descended from a common ancestor. Thus a natural classification becomes a genealogical tree, and the problem of classification is the tracing of its branches.

This, however, is a matter of extreme difficulty. Representing by a tree the whole of the animals which have ever lived on the earth, those existing at the present day would be figured by the topmost twigs, the trunk and main branches representing extinct forms. Thus the task of arranging animals according to their relationships would be an almost hopeless one but for two circumstances; one, that remains of many extinct forms have been preserved; the other, that the series of changes undergone by an animal in its development from the egg sometimes appears to afford an indication of the changes by which, in the course of ages, it has been evolved from an ancestral type. Moreover, the fully developed animal may exhibit vestigial structures which provide valuable clues as to its line of descent or its relation to other animals. The latter types of evidence are furnished by embryology and **Comparative Anatomy.** The study of extinct animals constitutes a special branch of morphology to which the name **Palæontology** is applied.

The solid crust of the earth is composed of various kinds of rocks divisible into two groups: (1) *Igneous rocks*, such as granite and basalt, the structure of

which is due to the action of the internal heat of the globe, and which originate below the surface and are not arranged in layers or strata; (2) *Aqueous* or *sedimentary rocks*, which arise by the disintegration, at the surface of the earth, of pre-existing rocks, the fragments or *débris* being carried off by streams and rivers and deposited at the bottom of lakes or seas. Being formed in this way by the deposition of successive layers or strata, the sedimentary rocks have a *stratified* structure, the lowest being in every case older than the more superficial layers. The researches of geologists have shown that there is a general *order of succession* of stratified rocks: that they may be divided into great *groups*, each representing an *era* of time of immense duration, and that each group may be subdivided into more or fewer *systems* of rocks, each representing a lesser *period* of time. The following table shows the principal rock-systems usually recognized, arranged under five great groups in chronological order, the oldest being at the bottom of the list.

Quarternary	Recent Pleistocene
Cainozoic or Tertiary	Pliocene Miocene Oligocene Eocene
Mesozoic or Secondary	Cretaceous Jurassic Triassic
Palæozoic or Primary	Permian Carboniferous Devonian Silurian Ordovician Cambrian
Pre-cambrian	

Imbedded in the rocks are found the remains of various extinct animals in the form of what are called *fossils*. In the more recent rocks the resemblance of these to the hard parts of existing animals is perfectly clear: we find shells hardly differing from those we pick up on the beach, bones easily recognizable as those of Mammals, Birds, or Fishes, and so on. But in the older rocks the fossils are in many cases so different in character from the animals existing at the present day as to be referable to no existing order. We find Birds with teeth, great aquatic Reptiles as large as Whales, Fishes, Molluscs, Crustacea, etc., all of an entirely different type from any now existing. We thus find that

the former were in many cases utterly unlike the present animal inhabitants of the globe, and we arrive at the notion of a *succession of life in time*, and are even able, in exceptionally favourable circumstances, to trace back existing forms to their extinct ancestors.

By combining the results of comparative morphology, embryology, and palæontology we get a department of zoology called **Phylogeny**, the object of which is to trace the pedigrees of the various groups. There are, however, very few cases in which this can be done with any approach to exactness: most "phylogenies" are purely hypothetical, and merely represent the views at which a particular zoologist has arrived after a more or less exhaustive study of the group under discussion.

Animals may also be studied from the point of view of **Distribution.** One aspect of this study is inseparable from Palæontology, since it is obviously necessary to mention in connection with a fossil the particular system or systems of rocks in which it occurs: thus we distinguish **geological distribution** or **distribution in time.**

The distribution of recent forms may be studied under two aspects: their **horizontal** or **geographical distribution** and their **vertical** or **bathymetrical distribution**. To mention the latter first, we find that some species exist only on plains, others—hence called *alpine forms*—on the higher mountains; that some marine shells, fishes, etc., always keep near the shore (*littoral* species), others live at great depths (*abyssal* species), while others (*pelagic* species) swim on the surface of the ocean. Among aquatic animals, moreover, whether marine or fresh-water, three principal modes of life are to be distinguished. There are animals, such as Jelly-fishes, which float on or near the surface of the water and are carried about passively by currents: such forms are included under the term *Plankton*. Most Fishes, Whales, and Cuttle-fishes, on the other hand, are strong swimmers, and are able to traverse the water at will in any direction; they together constitute the *Nekton*. Finally, such animals as Crabs, Oysters, Sponges, Zoophytes, etc., remain permanently fixed to or creep over the surface of the bottom, and are grouped together as the *Benthos*.

Under the head of geographical distribution we have such facts as the absence of all Land-mammals, except Bats, in New Zealand and the Polynesian Islands, the presence of pouched Mammals, such as Kangaroos and Opossums, only in some parts of America and in Australia and the adjacent islands, the entire absence of Finches in Australasia, and so on. We find, in fact, that the *fauna*—*i.e.*, the total animal inhabitants—of a country is to a large extent independent of climate, and that the faunæ of adjacent countries often differ widely. In fact, it is convenient in studying the geographical distribution of animals largely to ignore the ordinary division into continents, and to divide the land-surface of the globe into what are called *zoo-geographical* regions. The characteristics of these regions will be discussed in a future section; at present

it is only necessary, for convenience of reference, to give their names and boundaries.

1. The *Holarctic Region* includes the whole of Europe, Asia as far south as the Himalayas, Africa north of the Sahara, together with the corresponding portion of Arabia, and North America as far south as Mexico. For convenience of reference it is often customary to divide this region into two: its Eurasian portion is then called the *Palæarctic*, its American portion the *Nearctic* region.

2. The *Ethiopian Region* includes Africa south of the Sahara, Southern Arabia, and Madagascar with the adjacent islands.

3. The *Oriental Region* includes India, Ceylon, South China, the Malayan Peninsula, and what are known as the Indo-Malayan islands, *i.e.*, those islands of the Malayan Archipelago which lie to the west of a line—called *Wallace's line*—passing to the east of the Philippines, between Borneo and Celebes and between Bali and Lombok.

4. The *Australian Region* includes Australia, Tasmania, and the Austro-Mayalan islands, *i.e.*, the islands of the Malayan Archipelago lying to the east of Wallace's line.

5. The *New Zealand Region* includes New Zealand and the adjacent islands, such as the Chatham, Auckland, and Campbell groups.

6. The numerous groups of islands lying between Australia and Southern Asia to the west, and America to the east, are conveniently grouped together as the *Polynesian Region*.

7. The *Neotropical Region* includes the whole of South and Central America and part of Mexico.

The study of the factors governing the distribution of animals in space involves an analysis of the various relations of the organisms to their living and non-living environment. The term **Animal Ecology** is applied to this field of zoological research.

As it is impossible to have a right understanding of a machine without knowing something of its mode of action and the purpose it is intended to serve, so the study of an animal is imperfect without a knowledge of the functions performed by its various parts, and the way in which they work together. The aims of **Animal Physiology** are the accurate description and experimental analysis of these functions, and the study of the conditions which determine them.

The description and experimental study of certain types of reaction which the animal as a whole exhibits in response to environmental stimuli are generally called the study of **Animal Behaviour**. The term **Animal Psychology** is also used to designate this branch of experimental zoology.

The list of the various departments of zoological science is not yet complete. The analysis of the processes of organic evolution has opened up the wide field

of the study of inheritance comprised under the term **Genetics**. Similarly, the descriptive study of the embryonic development of the individual has led on to the **Experimental Analysis of Development** or **Experimental Embryology.** A central position amongst the various branches of descriptive and experimental biology is occupied by **Cytology**, the study of the structure and function of the cell as the structural and physiological unit of the living organism.

SECTION I

THE GENERAL STRUCTURE AND PHYSIOLOGY OF ANIMALS

1. AMŒBA.

IF we examine under the microscope a drop of water containing some of the slimy deposit which collects at the bottom of pools of rain-water and in similar situations, we occasionally find it to abound with living organisms of microscopic size. Amongst the great variety of such organisms to be found in our drop of water, *Amœba proteus* (Fig. 1) may at first sight easily be mistaken for a particle of non-living material. Its shape is irregular, and it appears to consist of some colourless, glass-like substance with a more granular central

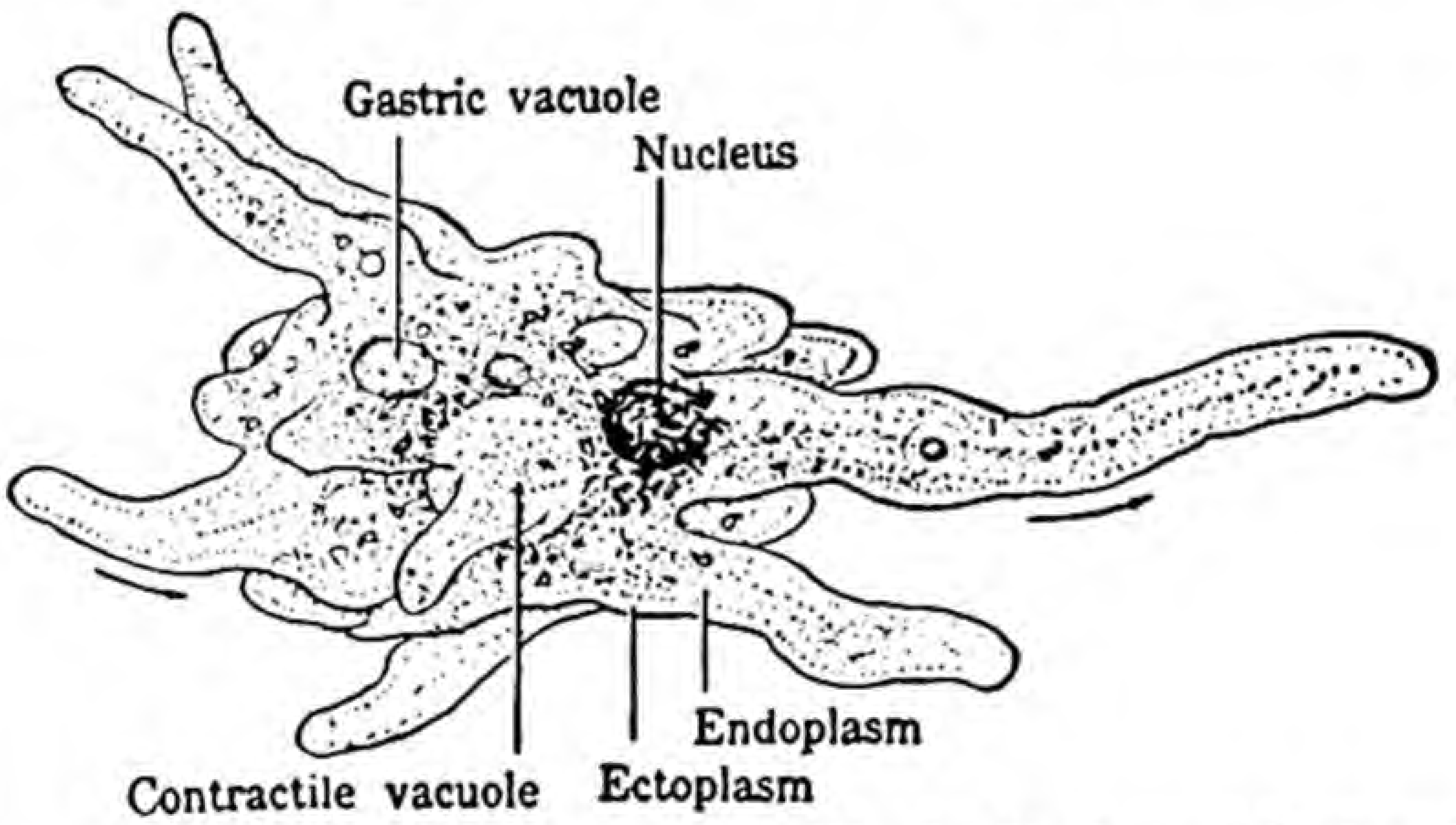


FIG. 1.—**Amœba proteus,** a living specimen. (From Woodruff's *Animal Biology* **(Macmillan Co.).)**

portion, and, on a cursory examination, we should most likely describe it as motionless. If, however, we make an exact drawing of the outline of the Amœba, and, after an interval, compare the drawing with the original, we find that the drawing appears no longer to represent what we see; a change has taken place in the shape of the Amœba; and careful observation shows that this change is constantly going on: the Amœba is constantly varying in shape. This change is effected by the pushing out of projections or processes, called pseudopods, which undergo various alterations of size and shape, and may become withdrawn, other similar processes being developed in their place. At the same time careful watching shows that the Amœba is also, with extreme slowness, changing its *position*. This it effects by a kind of streaming motion. A projection forms itself on one side, and the entire substance of the Amœba gradually streams into it; a fresh projection appears towards the same side, the streaming movement is repeated, and, by a constant succession of such

movements, an extremely gradual locomotion, which is often difficult to detect, is brought about. In these movements, it is to be noticed, the Amœba is influenced to some extent by contact with other minute objects; when the processes come in contact with small grains of sand or other similar particles their movements are modified in such a way that the Amœba, in its slow progress onwards, passes on one side of them, so that it might be said to feel its way among the solid particles in the drop of sediment. Experiments show that the direction of its movements is capable of being influenced from without by other agencies—by light and heat, for example. So that we are led to conclude that Amœba has a fairly wide range of *irritability* or sensitiveness to external influences or environment.

Judging from the nature of the movements, we are obliged to infer that the substance of which this remarkable organism is composed must be fluid, yet not miscible with water. It is a substance of complex chemical composition called *protoplasm*, which constitutes the vital material of all living organisms, whether animals or plants. In Amœba the protoplasm is in many cases clearly distinguishable into two parts: an outer homogeneous, glassy-looking layer (*ectoplasm*) completely enclosing a more granular internal mass (*endoplasm*).

Examination of the Amœba with a fairly high power of the microscope reveals the presence in its interior of two objects which with a low power we should be likely to overlook. One of these is a small rounded body with well-defined contour, which preserves its form during all the changes which the Amœba as a whole undergoes. This is termed the *nucleus* (Fig. 1); it is enclosed in an extremely delicate membrane, and contains a protoplasmic material differing from that which forms the main bulk of the Amœba in containing a substance which refracts the light more strongly and which has a stronger affinity for certain colouring-matters. The other minute object to be distinguished in the interior appears as a clear rounded space in the protoplasm. When this is watched it will be observed to increase gradually in size till it reaches a maximum of, let us say, a fifth of the total diameter of the Amœba, when, by a contraction of its walls, it suddenly disappears, to reappear presently and gradually grow again to its maximum size. This pulsating clear space is the *contractile vacuole*.

By watching the Amœba carefully for some time we may be enabled to observe that the movements of the protoplasm of the body not only effect locomotion, but are connected also with the uptake of food-particles into the interior of the protoplasm. When the Amœba meets with a minute animal or plant, or with minute fragments of larger forms, the region of the ectoplasm touching the foreign particle appears somewhat to soften, and the food-particle is subsequently surrounded by flowing protoplasm until it is completely drawn into the interior of the organism. There, a so-called *food-vacuole* is formed around it, into which some fluid appears to be liberated by the surrounding

protoplasm (Fig. 1, Gastric vacuole). From within this vacuole the food-particle subsequently disappears in part or as a whole. The disappearing matter evidently mixes with the protoplasm and adds to its bulk. All, in fact, of the matter of the food-particle which is capable of doing so is digested and assimilated by the protoplasm. The fluid in the food-vacuole probably contains some ingredient of the nature of an *enzyme*, which is able to act on certain substances and render them more soluble or capable of being more readily taken up by the protoplasm. This we infer mainly from what we know of the digestion and absorption of food in the higher animals; but the fact, which has been established by experiment, that the Amœba is able readily to digest certain classes of organic substances, while others, when taken into the interior of the protoplasm, remain unaltered, seems to indicate that some special property, similar to those possessed by the digestive enzymes of the higher animals, is present in the watery fluid surrounding the food-particle.

The movements of the Amœba, slow and gradual though they are, must involve a certain expenditure of energy. This energy is derived from chemical changes which go on in the protoplasm, or in close contact with it. Substances of complex chemical composition, such as carbohydrates, fats, and proteins, deal out energy while they are being split up into simpler compounds. The substances enumerated above can be said to provide the organism with potential energy, which on their decomposition and degradation is partly converted into the kinetic energy necessary for the various activities of the living organism.

A new supply of potential energy is constantly derived from ingested food-substances, which are also used in maintaining or increasing the bulk of the organism. If food-particles were absent from the water, the bulk of the Amœba would gradually diminish. The term *metabolism* has been assigned to the sum of the complicated chemical activities of living matter. Destructive metabolism or catabolism are the terms applied to the chemical changes that are involved in the splitting up of complex organic substances into compounds of a lower order. Immediately connected with the catabolic processes is the passage inwards of oxygen from the air dissolved in the water, and the passage outwards of carbon dioxide. Oxygen is a necessary agent in the process of destructive metabolism, and carbon dioxide is a constant waste-product of such action. This interchange of oxygen and carbon dioxide is the essence of the process of *respiration* observable in all living things. When Amœbæ are placed in water from which all atmospheric oxygen has been removed, all movement soon becomes arrested, the pseudopods become withdrawn, the body becoming rounded off and enclosed in a thin covering or *cyst*, and if the deprivation is made to last long enough death and disintegration follow. Similar results follow the presence of excess of carbon dioxide in the water. In such an environment the Amœba is unable to get rid of the carbon dioxide which it is itself producing, and becomes poisoned by the accumulation.

In addition to carbon dioxide given off in this process, other waste-products such as *urea* or *uric acid* are formed and have to be got rid of. The process of liberating such waste-products is called *excretion*.

When food is abundant the Amœba increases in bulk—more food being ingested than is required for simply maintaining the size unaltered—and soon a remarkable change takes place. The processes are withdrawn, and a fissure appears dividing the Amœba into two parts (Fig. 2). This fissure grows inwards, and the two parts become more and more completely separated from one another, till eventually the separation is complete, and we have two distinct

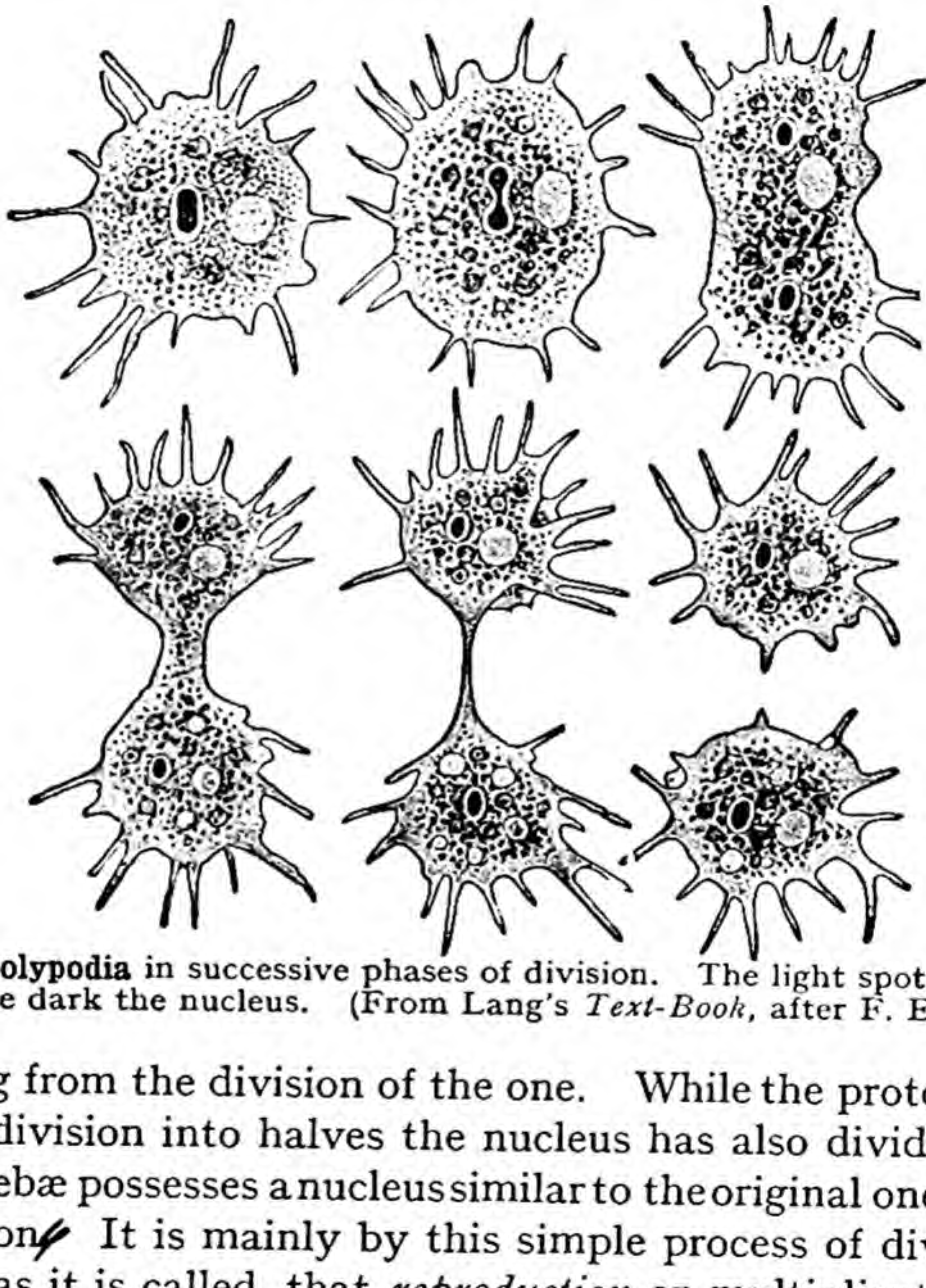


FIG. 2.—**Amœba polypodia** in successive phases of division. The light spot is the contractile vacuole; the dark the nucleus. (From Lang's *Text-Book*, after F. E. Schulze.)

Amœbæ resulting from the division of the one. While the protoplasm has been undergoing this division into halves the nucleus has also divided, and each of the two new Amœbæ possesses a nucleus similar to the original one, and developed from it by division. It is mainly by this simple process of division into two, or *binary fission* as it is called, that *reproduction* or multiplication takes place in the Amœba.

In spite of the great simplicity of its structure, the Amœba thus carries on a number of different functions. The practically structureless particle of protoplasm is able to act on matter absorbed as food in such a way as to alter the chemical composition of the latter and to assimilate it; it is able to carry on movements of locomotion, as well as movements—those involved in the taking in of food-particles—which may be looked upon as movements of prehension;

it exhibits a certain degree of sensitiveness or irritability, as shown by the modifications of its movements which result from contact with foreign bodies; it is able to respire; it carries on processes of excretion; and, finally, it is capable of reproducing its kind. It is these functions that characterize *living* beings as distinguished from *non-living* matter.

In connection with these vital processes of Amœba the nucleus plays an important rôle. If an Amœba be cut in two, the part containing the nucleus continues to comport itself like a normal complete animal; it continues to take in and digest food, and eventually recovers its original size. The non-nucleated part, on the other hand, though it may continue to live for a good many days, is unable to absorb nourishment; its movements lack co-ordination and it does not respond to stimuli in the normal way. Eventually death takes place in about ten to thirty days as a result, apparently, of the exhaustion of the store of potential energy—the processes of destructive metabolism having continued without the compensating processes of nutrition and assimilation.

In the course of our investigation we have recognized Amœba as a minute living being which, in spite of its apparently simple structure, performs in principle all known vital activities. The presence together of certain properties, such as the power of locomotion, the capacity of assimilating organic substances, the lack of two special compounds—chlorophyll and cellulose—justifies the inclusion of Amœba in the Animal Kingdom.

2. The Animal Cell.

In all but the lowest animals the various functions just enumerated are carried on by means of a more or less complex machinery of organs—*muscles, alimentary* or *enteric canal, glands, heart* and *blood-vessels, gills* or *lungs, nervous system, organs of excretion,* and *organs of reproduction.* But in all animals, however complex, the same substance, *protoplasm*, which in Amœba constitutes the bulk of the body, is the essential and active part. Wherever in the body active functions are being discharged and active changes are going on, there we find protoplasm present; where there is no protoplasm there is no vital activity. Protoplasm, as we have already seen, is a clear or finely granular substance which can be described as being of a fluid or, better, viscid consistency. It is not a definite chemical compound, but a highly organized mixture of complex chemical substances. Although it is impossible to associate the living state of protoplasm with any particular type of substance, it is safe to say that its most important constituents are of the nature of *proteins*. Proteins are substances of a high molecular weight, and are usually composed of the elements carbon, oxygen, nitrogen, hydrogen, sulphur, and traces of phosphorus. On drying up, protoplasm yields roughly 75 per cent. water, and the greater part of the dry residue can be shown to be protein. Only a small proportion consists of carbohydrates, fats, and salts. It is very difficult, if not even useless, to distinguish

amongst these substances between constituents immediately responsible for the vital activity of protoplasm, and such substances that would be described as mere accessories. Not only the chemical nature of the constituents is responsible for the maintenance of the living state, but also their physico-chemical and spatial arrangement—in other words, their *organization*.

In the living condition protoplasm is capable of *reversibly* passing from the viscid condition into a gelatinous one. It is, however, *irreversibly* coagulated by the action of heat, strong alcohol, and various other chemical substances, Since such coagulation can be made to take place causing relatively little deformation, this procedure is widely used in the preserving or *fixing* of protoplasmic material for the microscopic investigation of its minute structure.

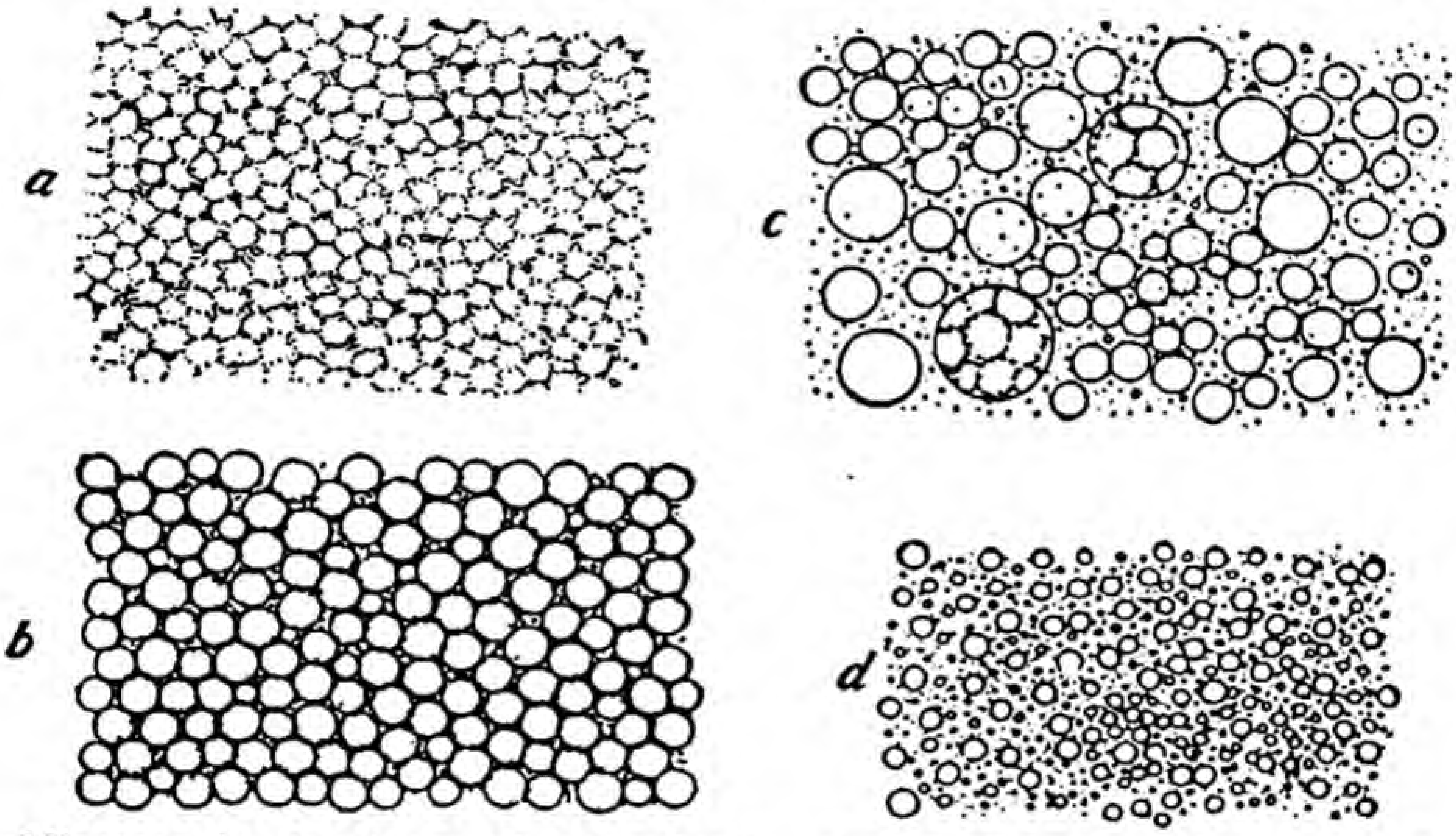


FIG. 3.—Microscopic structures of protoplasm. *a*, protoplasm of the egg of the sea-urchin (Toxopneustes) in section showing meshwork of microsomes; *b*, protoplasm from a living starfish egg (Asterias) showing alveolar spheres with microsomes scattered between them; *c*, the same in a dying condition after crushing the egg; alveolar spheres fusing to form larger spheres; *d*, protoplasm from a young ovarian egg of the same. (From Wilson's *The Cell in Development and Heredity* (Macmillan Co.).)

As regards the microscopically visible structure of protoplasm a wide diversity of opinion has been derived from the study of both fixed and living material. Under the microscope protoplasm usually appears to be a fine dispersion of globules and other minute particles freely suspended in a liquid medium. The size of the particles may range from the limit of visibility to a maximum of approximately 10μ in diameter. The larger particles are clearly distinguishable as fluid droplets, and even the smallest particles, which are usually called granules, have been shown to be of a fluid nature. It can be concluded from this that protoplasm in its gross structure represents what is commonly called an *emulsion*. The term *alveolar* has been used to designate this kind of visible structure (Fig. 3b). Mainly on the basis of the study of the fixed material, a number of rival structures of the protoplasm (fibrillar, reticular or net-like, and sponge-like) have been postulated. In many cases it was, however, possible

to explain these structural configurations as special forms of appearance of the emulsion type of structure.

In general it is impossible to attribute to living protoplasm any constant, microscopically visible, structure. As to its ultramicroscopical structure, no direct evidence exists. The free flow of protoplasm on the one hand, and its rigidity and elasticity on the other, have led to the conclusion that one deals with an elastic colloidal system built up of linear crystalline units (protein-molecules or molecule-chains), which in their way of intermeshing may be compared with a loosely-put-together *brush-heap* (Fig. 4). Such a structure would explain the strange concurrence of the above-mentioned mechanical properties of protoplasm—fluidity and elasticity—which at first sight would seem mutually to exclude one another.

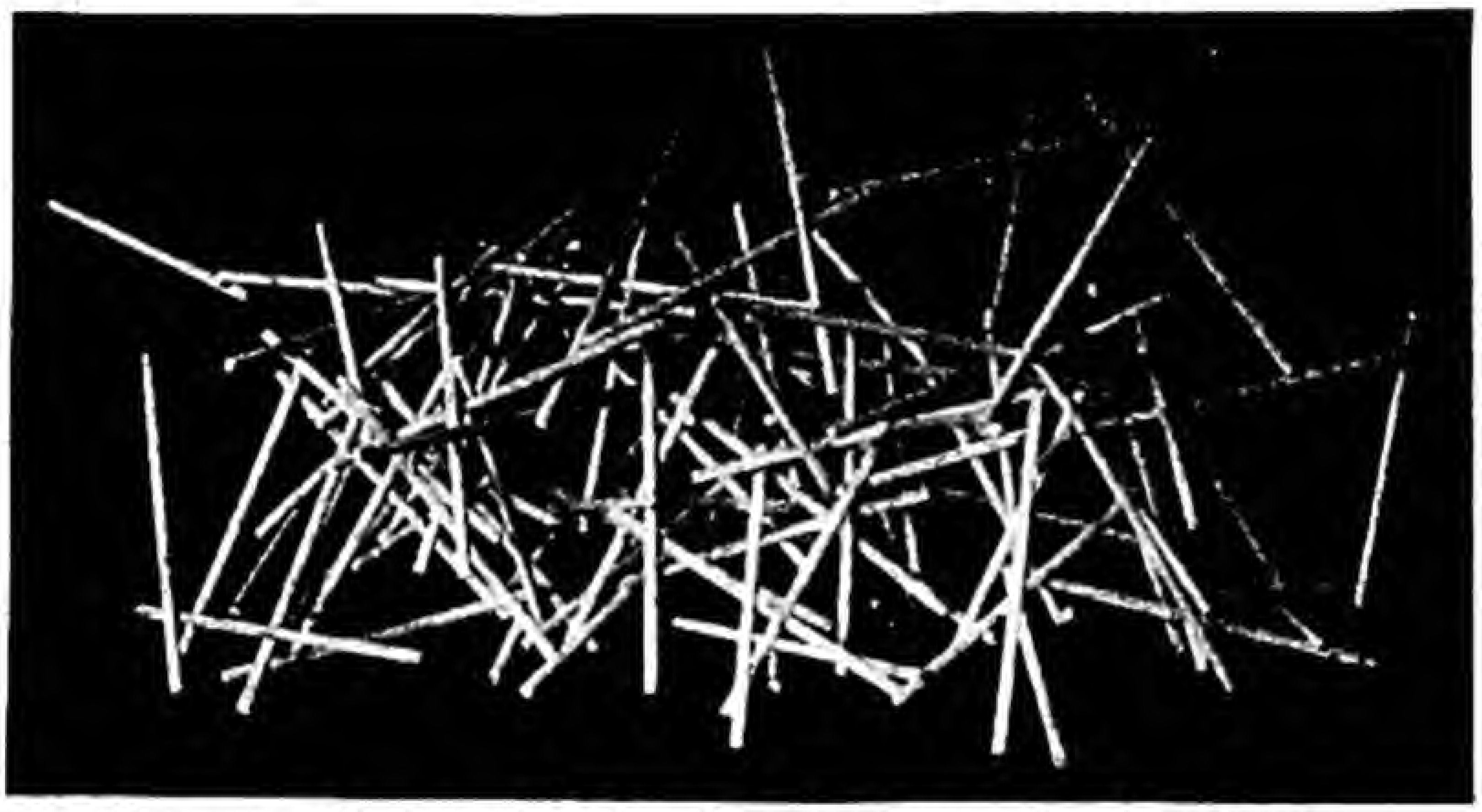


FIG. 4.—Model of molecular structure of protoplasm. (From Seifriz's *Protoplasm* (McGraw-Hill).)

We have already seen that a particle of protoplasm containing a nucleus in its interior constitutes the entire body of an Amœba. The smallest unit of which the body of a more highly differentiated plant or animal is made up likewise consists of a minute portion of protoplasm surrounding a nucleus. To such a structural element the term *cell* is applied. The word was first employed in reference to the microscopic structure of plants in connection with which it is more appropriate than in connection with the microscopic structure of animals; for a plant-cell has nearly always a definite, firm, enclosing envelope or *cell-wall* (Fig. 5), a structure which is only exceptionally present in animal cells. The nucleus in the interior of the cell-protoplasm or *cytoplasm* is mostly, as in Amœba, of a rounded shape, and appears to be surrounded by a thin nuclear membrane. The nucleus contains a very complex protoplasmic material termed *chromatin*, which has a marked affinity for certain dyes. Part of the chromatin shows an affinity to *basic* dyes, and is therefore called *basichromatin*. This represents the chromatin proper of the older school of cytologists. Another portion of nuclear chromatin is, like the cytoplasm, readily stained by *acidic*

dyes, and is called *oxychromatin*. The nuclear substance known by the name *linin* has the properties of oxychromatin. The two kinds of chromatic material have been shown to be able to change into one another. This explains the common application of the term chromatin to the whole of the stainable substance of the nucleus. The nucleus contains, further, a more or less microscopically homogeneous and unstainable ground-substance, which is usually called *nuclear sap*, although nothing definite is known about its consistency.

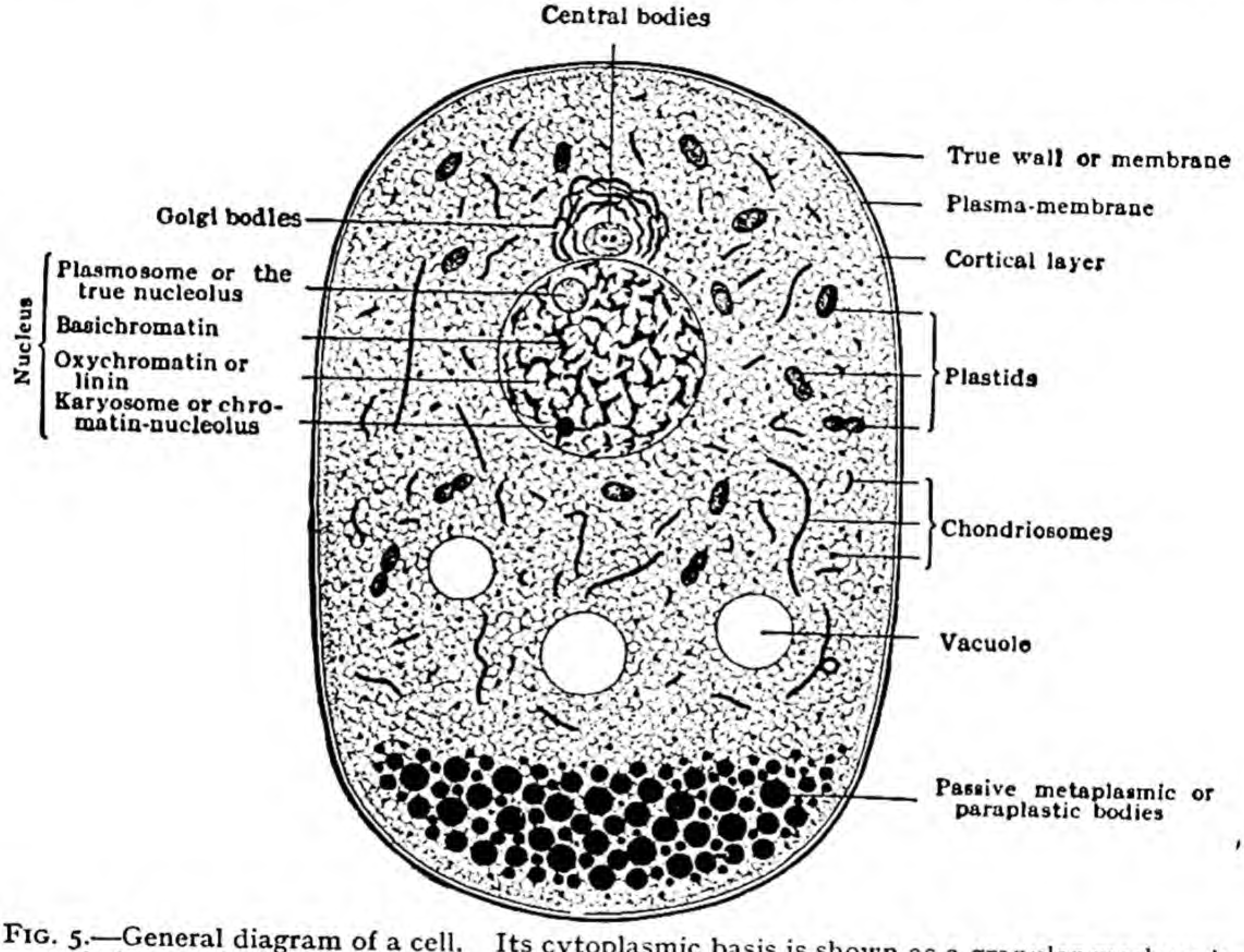


FIG. 5.—General diagram of a cell. Its cytoplasmic basis is shown as a granular meshwork or framework in which are suspended various differentiated granules, fibrillæ and other formed components. (From Wilson's *The Cell in Development and Heredity* (Macmillan Co.).)

The arrangement of these constituents differs greatly in different nuclei and in the same nucleus at different times.

In the resting condition of the nucleus—*i.e.*, when cell-division is not in progress—the basichromatin may be distributed in the form of granules throughout the nucleus; it may, or more rarely may not, be connected with a network of linin. Thus, in a typical resting nucleus these granules appear to be strung along threads of linin, so that the basichromatin stands out as a conspicuous network. This type of nucleus, called the *vesicular* type, is of general occurrence in the tissue-cells of most cellular animals and plants. In the nuclei of many unicellular animals—*i.e.*, animals in which, as in Amœba, the whole body

resembles a single animal cell—the chromatin is concentrated in a relatively large central mass. Such nuclei usually appear homogeneous, and are stained with great intensity by basic dyes; they are called *massive nuclei*. Finally, in certain unicellular organisms, small granules of chromatin, so-called *chromidia* or *chromioles*, or larger irregular lumps of chromatin are scattered through the protoplasm without forming a single individual nucleus at all.

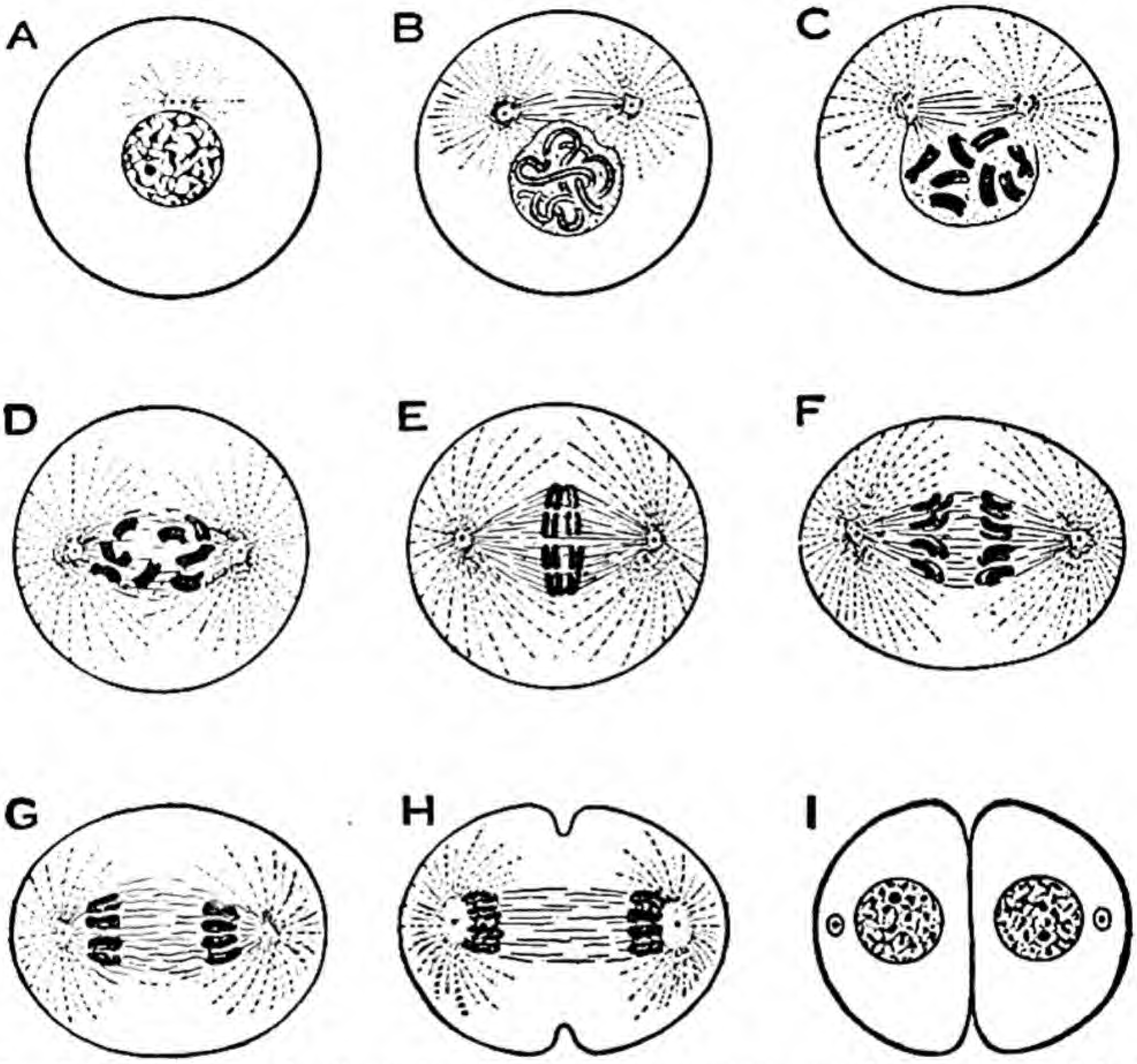


FIG. 6.—Typical stages of mitosis in which the chromosome number is assumed to be eight. *A*, prophase (start): chromatin still exhibiting net-like arrangement, centrosome divided and surrounded by aster; *B*, prophase (early): chromatin in spireme form, centrosomes moving apart and spindle arising between; *C* and *D*, prophases (later): nuclear membrane disappearing, constituent chromosomes of spireme separating; *E* and *F*, metaphase and anaphase (early): chromosomes are arranged in equatorial plate and each separating into two along a longitudinal split; *G*, anaphase (later): a set of eight chromosomes approaching each aster; *H*, telophase: gradual loss of visibility of distinct chromosomes, asters and spindle disappearing, division of cytoplasm beginning; *I*, mitosis completed, two cells. (From Woodruff's *Animal Biology* (Macmillan Co.).)

Most nuclei, especially those of higher organisms, contain almost invariably one or more, sometimes numerous, rounded bodies, the so-called *nucleoli* (Fig. 5). Two kinds of nucleoli are generally distinguished: nucleoli staining with acidic dyes—viz., *plasmosomes*—and others staining with basic dyes—viz., *karyosomes*. Their significance is still imperfectly understood.

When the nucleus divides during the process of division of the cell, its con-

tents go through a remarkable series of changes, to which the term *mitosis* or *karyokinesis* is applied. At the time when this mitotic division is being initiated, either one or two minute bodies intensely staining with certain dyes are to be distinguished situated in the cytoplasm in the immediate neighbourhood of the nucleus. When only one of these bodies is present at the outset, it subsequently becomes divided into two. These are the *central bodies* consisting of a minute, deeply staining corpuscle, which is often surrounded by a lighter zone, the so-called *centrosphere*. Each central body may be found to be the focus of a system of very fine fibres of protoplasmic material, termed *astral rays*, forming a structure known as the *aster*. The central bodies, at first close together, gradually separate from one another, a splinde-shaped bundle of plasmatic fibrils, the so-called *spindle-fibres* extending between them (*amphiaster*).

Meantime important changes have been in progress in the nucleus. The linin-network with its attached chromatin-granules first becomes arranged in a close tangle (*spireme*), and then becomes divided up in a very definite and orderly manner into a number of parts, the *chromosomes*. These have frequently the form of loop-like threads, but often assume other forms. A constant number of chromosomes is found in all body-cells of an animal, this number being characteristic of the species to which the animal belongs. At the time of the appearance of the chromosomes the nuclear membrane disappears. Each of the chromosomes splits lengthwise into two parts, the daughter-chromosomes, and with these the fibres of the spindle become connected (*prophase*, Fig. 6, *A–D*). Now the longitudinally divided chromosomes take up a position in the equatorial plane of the spindle, to form a single group—the *equatorial plate*. The spindle has shifted its position, so that its fibres now run across the original site of the nucleus (*metaphase*, Fig. 6, *E*). Each daughter-chromosome now separates from its fellow, so that two groups are formed, each containing a similar number of chromosomes. The two groups then move apart from one another, each approaching the corresponding end or pole of the spindle (*anaphase*, Fig. 6, *F*, *G*). How this movement is effected is not definitely known.

When the groups of chromosomes have approached the opposite spindle-poles, they unite, and eventually the entire chromosome-material of each of the two groups assumes the arrangement which it exhibited before the division of the original nucleus began (*telophase*, Fig. 6, *H*, *I*). At last a new nuclear membrane is formed around each daughter-nucleus. It is of importance to note that, though in this mitotic division of the nucleus of the animal cell the central bodies are so conspicuous that it would appear as if they had an important share in controlling the process, yet mitosis takes place during cell-division of the higher plants on the same general lines as in animals, though centrosomes have rarely, if ever, been observed in plants higher than the Mosses.

Towards the end of the anaphase a furrow appears around the cell-body, form-

ing a ring in a plane at right angles to the long axis of the spindle. This furrow deepens gradually so as to give rise to a cleft, eventually completely separating the substance of the cell into two halves. Each of these halves encloses one of the daughter-nuclei, and has assumed the character of a complete *daughter-cell*.

In some instances the division of the nucleus is *direct* or *amitotic*, the nucleus simply becoming separated into two equal parts, without disappearance of the nuclear membrane and without any complicated re-arrangement of the chromatin.

3. Germ-Cells: Maturation, Fertilization and Cleavage. The Germinal Layers.

Amœba can be compared to a single animal cell, and is usually described as a unicellular animal. As such it is a member of the phylum Protozoa. All the rest of the animal kingdom, forming the divisions Parazoa and Metazoa, are multicellular in the fully developed condition; but in the great majority of these multicellular animals the life-history of the individual starts from the fertilized egg or *zygote*, which, like Amœba, is comparable to a single cell.

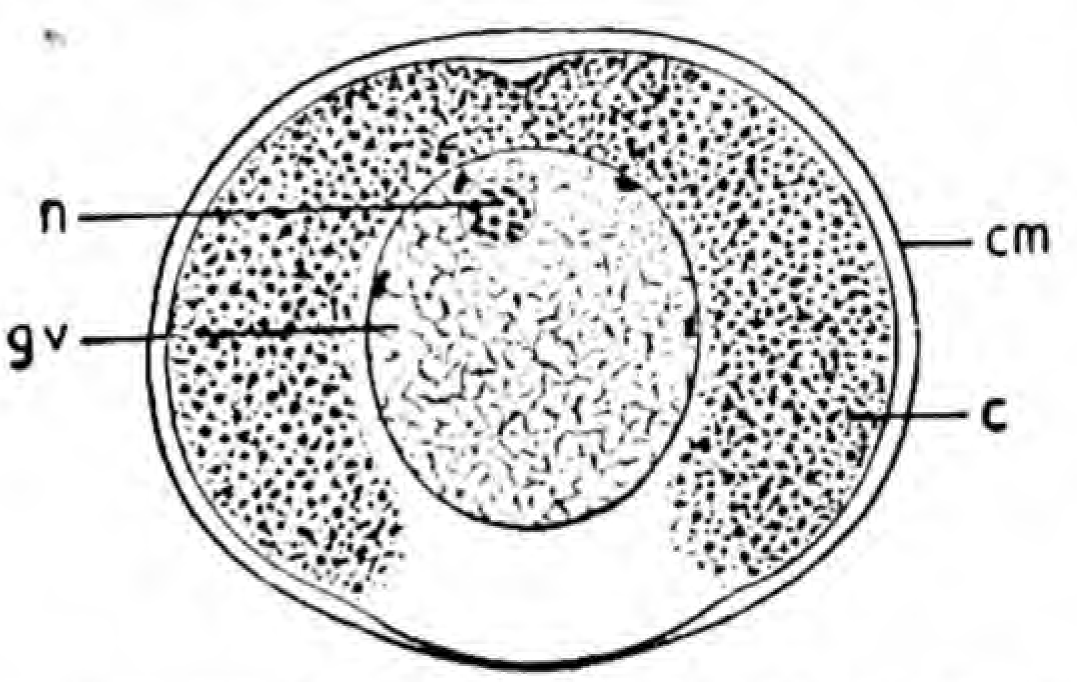


Fig. 7.—Ovum of a mollusc (Dentalium) showing the cell membrane (*cm.*), the cytoplasm (*c.*) containing yolk granules, the large nucleus (germinal vesicle, *gv.*) with its nucleolus (*n.*). (From Wilson's *The Cell in Development and Heredity* (Macmillan Co.).)

The zygote is the product of *fertilization*—*i.e.*, of the fusion of the female germ-cell, the egg or *ovum*, with the male germ-cell, the *sperm*. The two kinds of germ-cells or *gametes* differ in size and shape, and in their mode of maturation.

The ovum is a typical cell (Fig. 7), usually of a very large size, with one or more enclosing membranes (*cm.*). The cytoplasm encloses a nucleus (*germinal vesicle*, *gv.*), which contains one or more nucleoli (*n.*). In addition to the cytoplasm (*c.*), the ovum usually contains a quantity of non-protoplasmic nutrient material called yolk.

The ova are developed in the female gonad, the ovary, from primordial germ-cells called *oogonia* (Fig. 8, *og.*). After a period of multiplication by mitotic divisions, the oogonia enter upon a growth period. They are now called *oocytes* (*oc.*). From them the mature ova are finally derived by two successive divisions, the *maturation divisions*. One of these differs entirely from an ordinary mitotic cell division, since it involves a reduction of the number of chromosomes to one half of the original number (*meiotic* division).

During the maturation division the nucleus of the oocyte approaches the surface and divides into two parts. One part comes to project on the surface, and finally the projection is completely separated off from the ovum as a

rounded particle, the first *polar body* (*p. b.*). In the second division of the nucleus a second polar body is thrown off in the same manner, and the first polar body may simultaneously divide again. Thus the mature ovum (*o.*) is of much the same size as the oocyte, from which it takes its origin, and bears on its surface two or three small rounded particles—the polar bodies.

After this the portion of the nucleus which remains in the ovum resumes its central position and forms what is termed the female pronucleus. It contains half the original number of chromosomes.

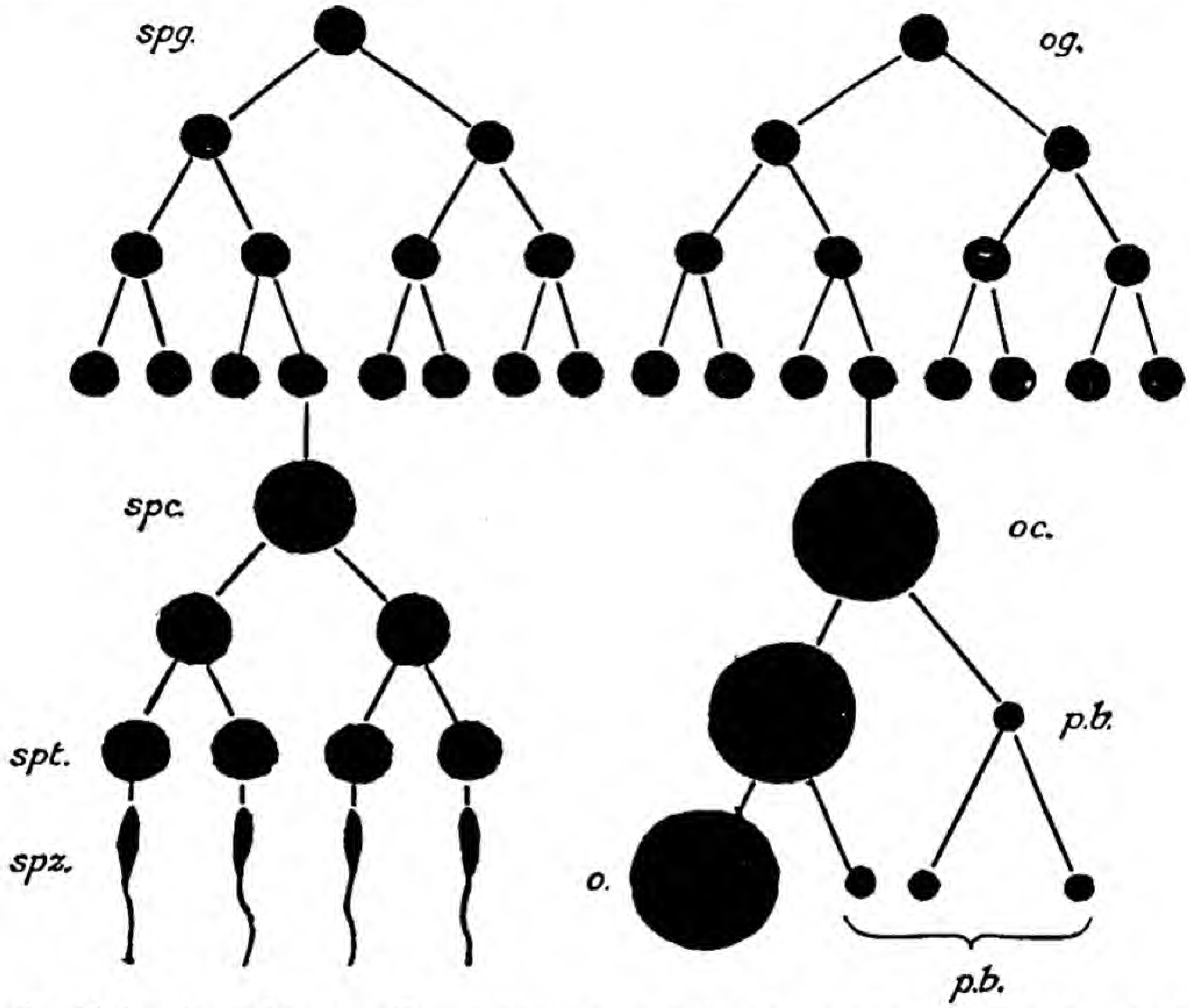


FIG. 8.—Maturation of germ-cells. *o.* ovum; *oc.* oocyte; *og.* oogonium; *p. b.* polar bodies; *spc.* spermatocyte; *spg.* spermatogonium; *spt.* spermatids; *spz.* spermatozoa. (Modified after Jenkinson.)

The *sperms* or *spermatozoa* (Fig. 9) are extremely minute bodies, nearly always motile, usually slender and whip-like, tapering towards one end, and commonly with a so-called head (*h.*) at the other end. Between the head and the tail (*t.*) a neck (*n.*) and a middle-piece (*m.*) are usually distinguishable.

The sperms develop in the male gonad—the *testis*—from primordial germ-cells, the *spermatogonia* (Fig. 8, *spg.*). These, too, first multiply by mitotic divisions, and then enter upon a period of growth which is, however, much shorter than the similar growth period in the ovum. The cells are now called *spermatocytes* (*spc.*). Two maturation divisions, one of which is of the meiotic type (reduction of the chromosome number by one half), lead to the formation

of the so-called *spermatids* (*spt.*), which finally assume the characteristic appearance of spermatozoa (*spz.*).

It is clear from the foregoing that in the development of the ovum one oocyte gives rise to one mature ovum only, whereas in the sperm-formation one spermatocyte gives rise to four mature spermatozoa.

In the process of fertilization (Fig. 10) the sperm penetrates into the interior of the ovum (*A*), and the sperm nucleus, which is now called the *male pronucleus*, advances towards the *female pronucleus*. As it does so, it is preceded by its central body, which is surrounded by a typical aster (*B*, *C*). The two pronuclei then conjugate, the male aster divides to form an amphiaster and the nuclei finally fuse more or less completely (*D*). In many animals, however, the sperm enters the ovum before the formation of the polar bodies. In these cases the male pronucleus rests inside the ovum until the female pronucleus is formed.

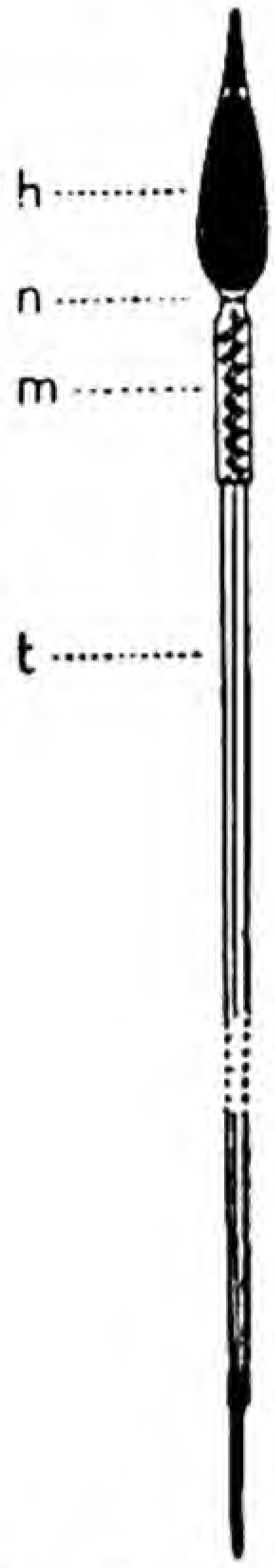


FIG. 9.—Diagram of animal sperm, based on the conditions found in mammals. A long section of the tail, indicated by dotted lines, is omitted. *h*. head; *m*. middle-piece; *n*. neck; *t*. tail. (From Wilson's *The Cell in Development and Heredity* (Macmillan Co.).)

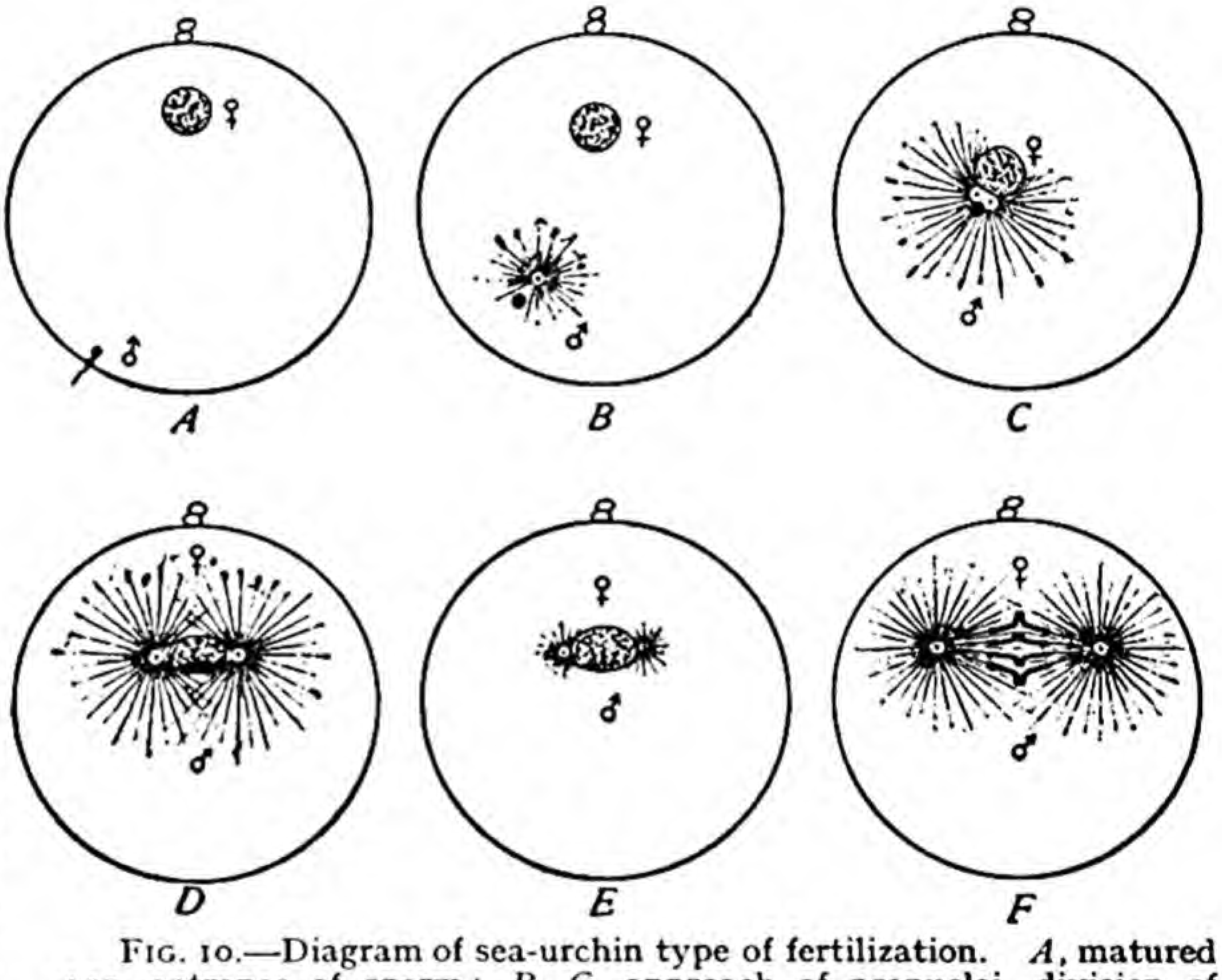


FIG. 10.—Diagram of sea-urchin type of fertilization. *A*, matured egg, entrance of sperm; *B*, *C*, approach of pronuclei, division of sperm-centre; *D*, sperm-aster divided, fusion of pronuclei; *E*, fusion-nucleus, reduction of asters; *F*, first cleavage figure. (From Wilson's *The Cell in Development and Heredity* (Macmillan Co.).)

The product of the pronuclei is the *fusion-nucleus* (*E*). It is to be noted that in this fusion the chromosomes of the male and female pronuclei do not fuse, but remain separate. The fertilized ovum is now called the zygote, and its nucleus contains the full number of chromosomes characteristic of the species.

Fertilization is shortly followed by the early development of the new organism. This is initiated by a process of repeated mitotic cell-divisions which is known as *cleavage* (Fig. 11). This either affects the entire substance (*holoblastic* or *complete* cleavage) or only a part (*meroblastic* or *incomplete* cleavage) of the zygote. In the former case the ovum usually contains com-

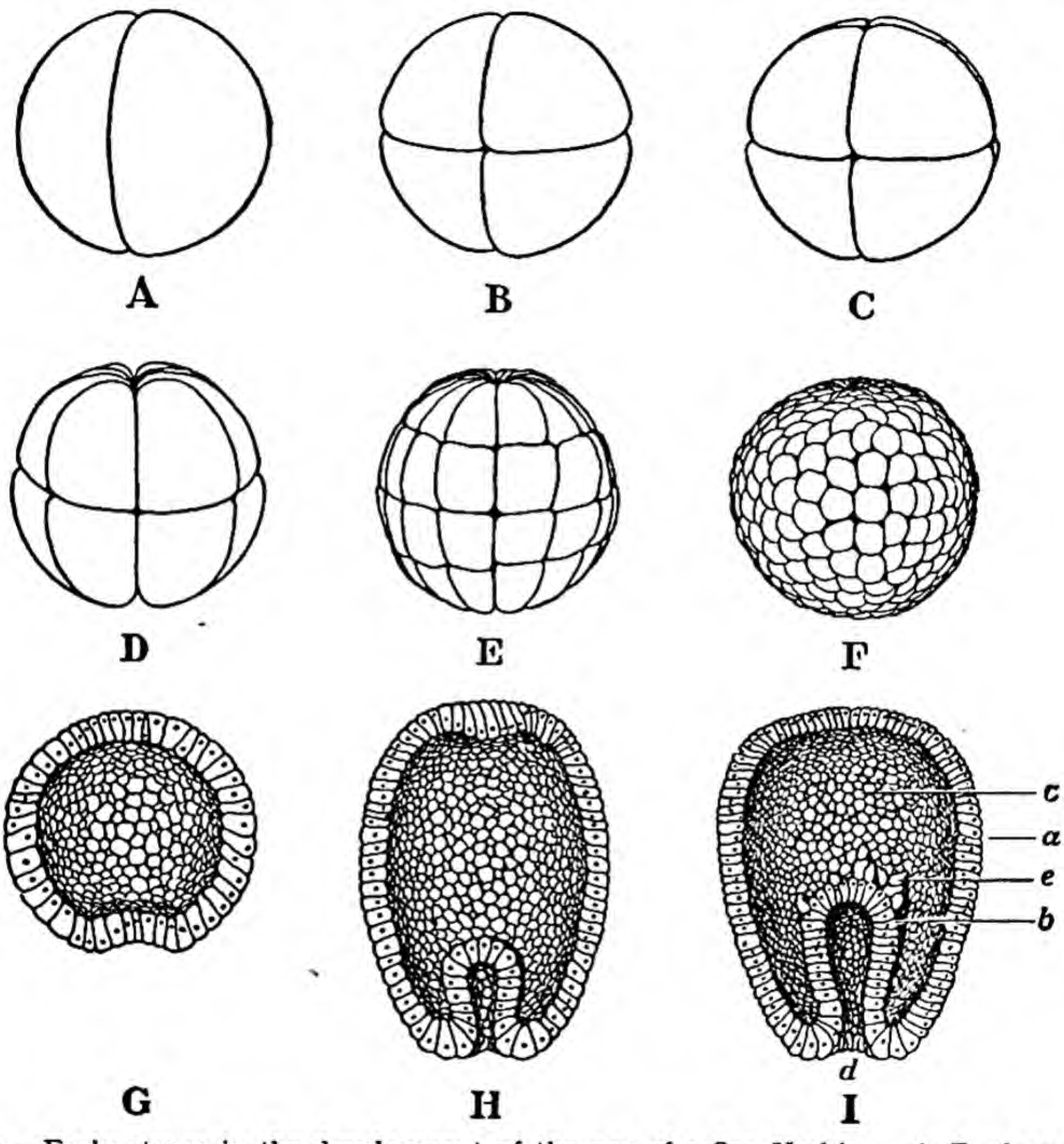


FIG. 11.—Early stages in the development of the egg of a Sea Urchin. *A–F*, cleavage and formation of the blastula; *G*, section of blastula showing beginning of gastrulation; *H–I*, early and later gastrula stages; *a*, ectoderm; *b*, endoderm; *c*, blastocoele; *d*, blastopore, leading into the enteric cavity; *e*, cells, arising from the endoderm, destined to form the mesoderm. (From Woodruff's *Animal Biology* (Macmillan Co.).)

paratively little or no food-yolk, consisting mainly of protoplasmic matter. The first stage in the process of cleavage is the mitotic division of the zygote nucleus, accompanied by the division into two parts of the substance of the protoplasm—the result being the formation of two cells, each with its nucleus (Fig. 11). Each of these two cells then divides—four cells being thus formed; the four divide to form eight; the eight divide to form sixteen, and so on; until, by the process of division and subdivision, the zygote becomes cleaved

into a large number of comparatively small cells which are termed the ***blastomeres***. This mass of cells is spherical in shape, and the rounded blastomeres of which it is composed project on its surface so as to give it somewhat the appearance of the fruit of the mulberry, whence it is termed the ***mulberry body*** or *morula* stage. The blastomeres next become arranged regularly in a single layer—the embryo assuming the form of a hollow sphere, the ***blastosphere*** or *blastula*, with a wall composed of a single layer of cells enclosing a cavity—the *segmentation cavity* or *blastocœle* (Fig. 11, *A–F*).

One side of the hollow blastula next becomes pushed inwards or ***invaginated*** (Fig. 11, *G–I*), as one might push in one side of a hollow india-rubber ball, the result of this process of invagination, or *gastrulation* as it is termed, being the formation of a cup—the *gastrula* (Fig. 12)—with a double wall. The cavity of the cup-shaped gastrula is the ***archenteron*** or primitive digestive cavity; the opening is termed the *blastopore*; the outer layer of the wall of the cup is the *ectoderm* (or *epiblast*), the inner the *endoderm* (or *hypoblast*). The ectoderm and endoderm are the ***primary germinal layers*** of the embryo; from one or both of them are developed the cells of a third layer—the *mesoderm* (*mesoblast*)—which is subsequently formed between them.

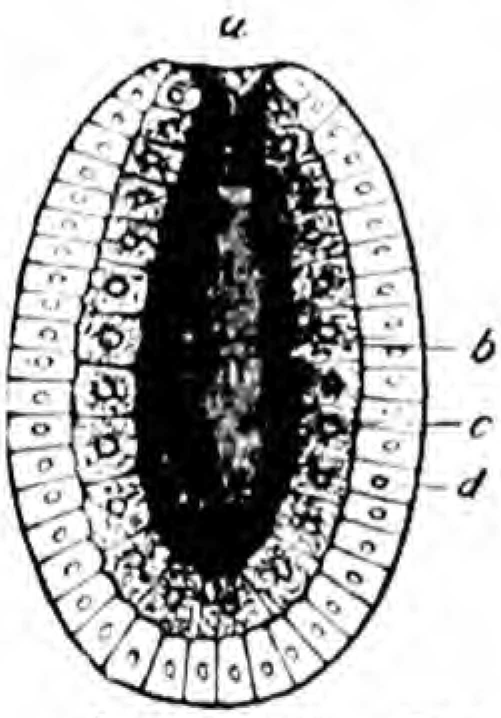


FIG. 12.—Gastrula in longitudinal section. *a*, blastopore; *b*, archenteron; *c*, endoderm; *d*, ectoderm. (From Gegenbaur's *Comparative Anatomy*.)

This mode of formation of the primary germinal layers in holoblastic zygotes by a process of gastrulation prevails in a number of different sections of the animal kingdom. In many animals, however, it becomes modified or disguised in various ways.

The cells of the three germinal layers give rise to the various organs of the body of the fully-formed animal—each layer having a special part to play in the history of the development. As the various parts of the embryo become gradually moulded from the cells of the germinal layers, it becomes evident on comparison that their internal structure—the form and arrangement of their constituent cells—is undergoing gradual modifications, the nature of which is different in the case of different parts. A *differentiation* of the cells is going on in the developing organs, resulting in the formation of a variety of different kinds of *tissues*.

4. TISSUES.

The cells of the tissues of the animal body differ greatly in form in different cases. Some are rounded, others cubical, others polygonal; some are shaped like a pyramid, others like a cone, others like a column or cylinder; others are flattened and tabular or scale-like. Some are amœba-like or *amœboid*, resembling Amœba in their capacity for developing pseudopods. Cells situated

on free surfaces are in many cases beset at their free ends with delicate, hair-like structures or *cilia* which vibrate to and fro incessantly during the life of the cell (Fig. 13, *c*); sometimes there is on each cell a single, relatively long, whip-like cilium, which is then termed a *flagellum* (*e*, *f*). Cells provided with cilia are termed *ciliated*, such as bear flagella *flagellate* cells.

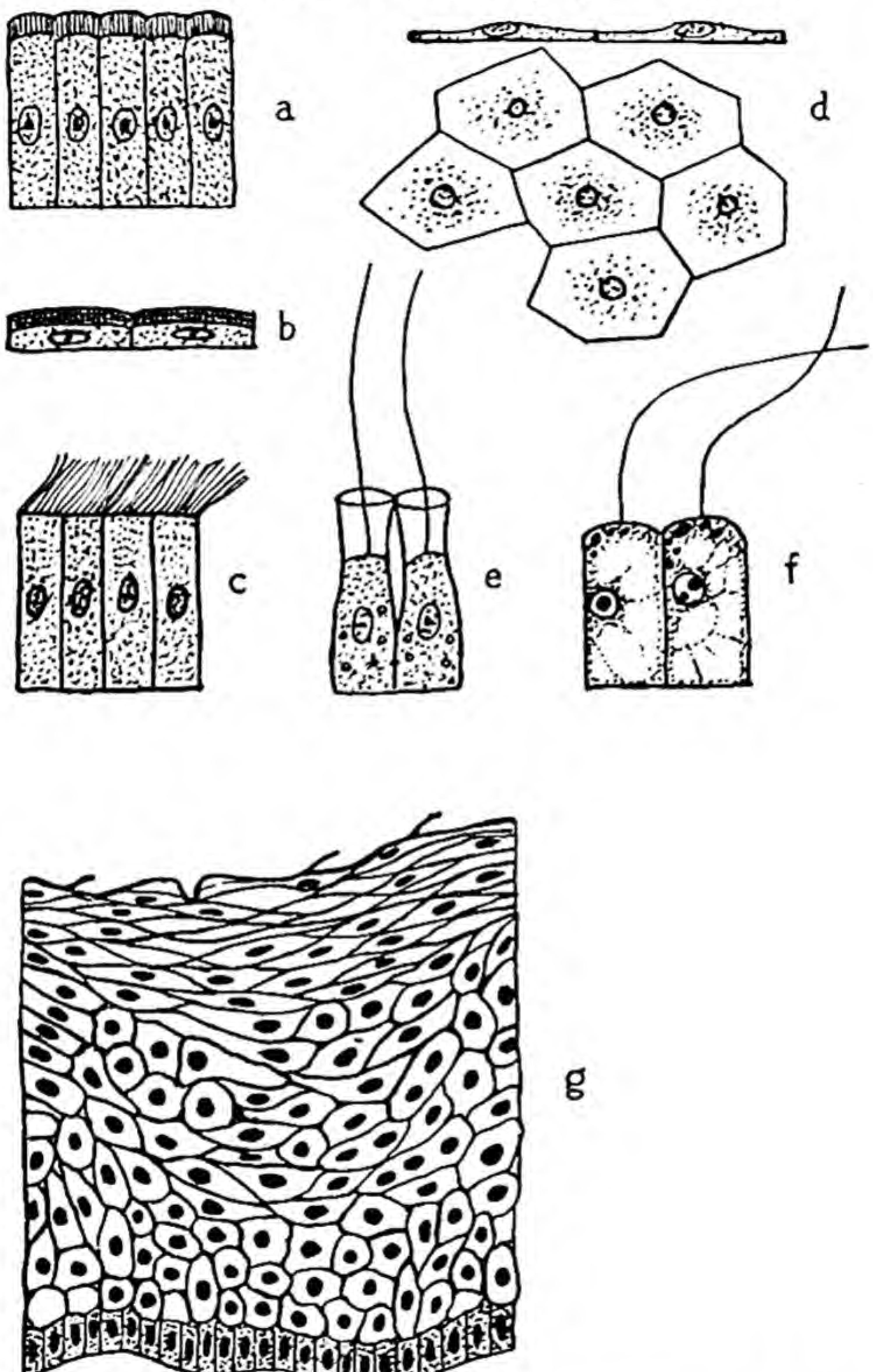


FIG. 13.—Various forms of epithelium. *a*, columnar epithelium; *b* and *d*, flattened epithelium; *c*, ciliated epithelium; *e* and *f*, flagellate epithelium; *g*, stratified epithelium. (After various authors.)

Some tissues are composed entirely of cells. Other tissues, though originating from cells or by the agency of cells, consist in greater or less measure of non-protoplasmic matter formed between the cells. Usually the component cells of a tissue are distinct; but there are many examples of tissues in which the cells have coalesced into an aggregation in which cell boundaries have

disappeared and the nuclei alone indicate the originally separate elements; such a structure is termed a *syncytium*.

The cells of which the tissues are composed are more or less highly differentiated for the performance of various special functions. In accordance with their functions, the tissues can be subdivided into the following groups: *epithelial* tissues, whose function may either be protective or glandular; *connective* tissues, which form the supporting structures of the body; *contractile* tissues, on which depend motion and locomotion; *conducting* tissues, which serve in the co-ordination of the various functions of the body; finally *reproductive* tissues, from which the germ-cells take their origin.

Tissues composed entirely of cells take the form, for the most part, of membranes covering both the external surface of the body and the surface of the body cavities. Such membranes are known under the general name of **epithelia.** The epithelial tissues may consist of a single layer of cells (Fig. 13, *a–f*) or may be many-layered (*g*); the former are termed *non-stratified*, the latter *stratified* epithelia.

The function of an epithelium may be simply to cover or protect the underlying parts of the body. In such cases the epithelial cells are often capable of producing protective substances such as horn or chitin. Epithelia consisting more or less of ciliated cells can have a locomotory function when lining the external body-surface, or when lining internal surfaces they may serve in the transport of fluids within the body-cavities.

Amongst the cells of both external and internal epithelia there are some which show a high degree of selective sensitivity to changes in mechanical pressure, in the temperature, the illumination, or the chemical composition of the environment. These epithelial cells are called *sensory cells*. At their free end they frequently bear hair-like processes which are obviously important in the reception of stimulation (Fig. 29). A further peculiarity of these cells is their power of handing on the effect of stimulation to the nervous tissue (*vide infra*) with which they are always closely connected.

Epithelial cells, which are capable of liberating or secreting through their surface substances usually formed in their interior, are called *glandular* cells. They are found scattered or in groups, forming respectively unicellular or multicellular glands. In the latter case a number of cells are found lining a depression or more or less complicated infolding of an epithelium. The secretion liberated by the glandular cells collects in the central cavity of the infolding and reaches the surface of the body or body-cavity through a narrow passage or duct (Fig. 14). There are, however, so-called *ductless glands* which liberate their secretion into the blood-stream. They, too, are generally of epithelial origin.

A series of tissues in which the cells are, in most instances, subordinate, as regards bulk, to substances formed between them, is the group known as the

connective or supporting tissues, including *gelatinous connective tissue, reticular connective tissue, fibrous connective tissue, cartilage,* and *bone.* In the majority of forms of connective tissue the cells lie embedded in an intermediate substance called the *matrix* or ground-substance.

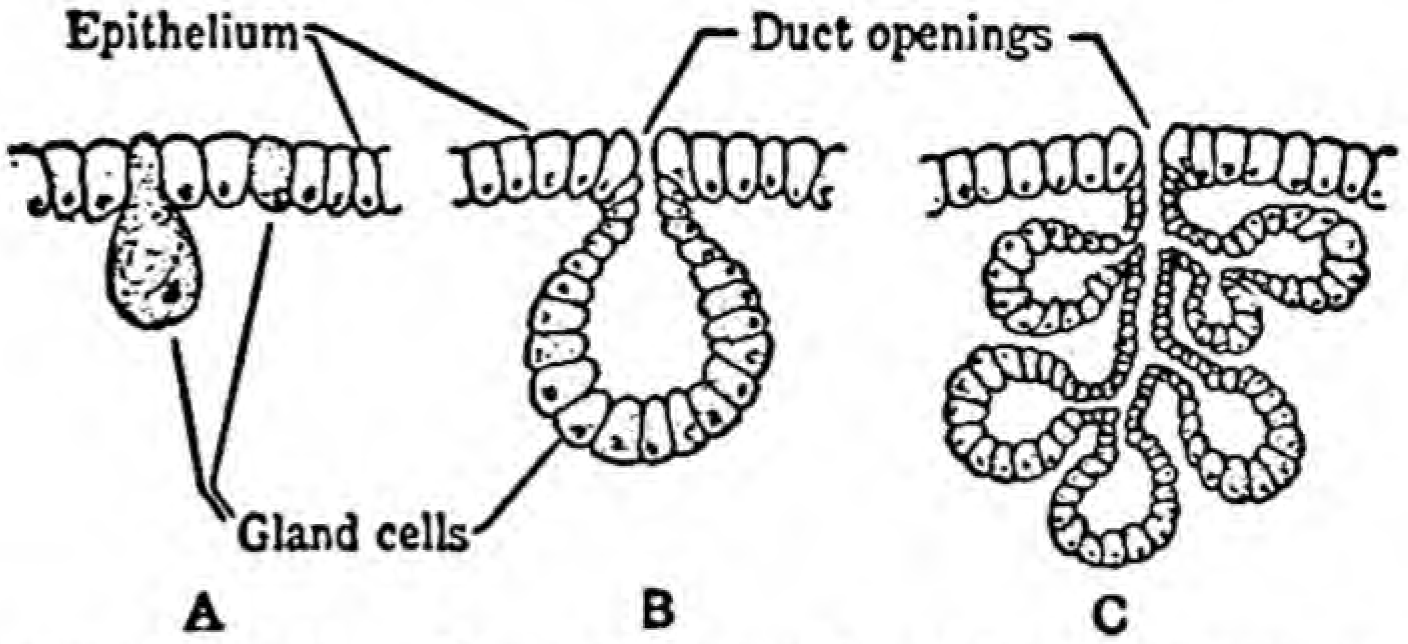


FIG. 14.—Diagram of glands. (From Woodruff's *Animal Biology* (Macmillan Co.).)

In the case of *gelatinous connective tissue* (Fig. 15) the ground-substance is of a gelatinous character, sometimes supported by systems of fibres, and the cells are usually stellate or star-shaped with radiating processes. *Reticular connective tissue* (Fig. 16) consists of stellate or branching cells with processes

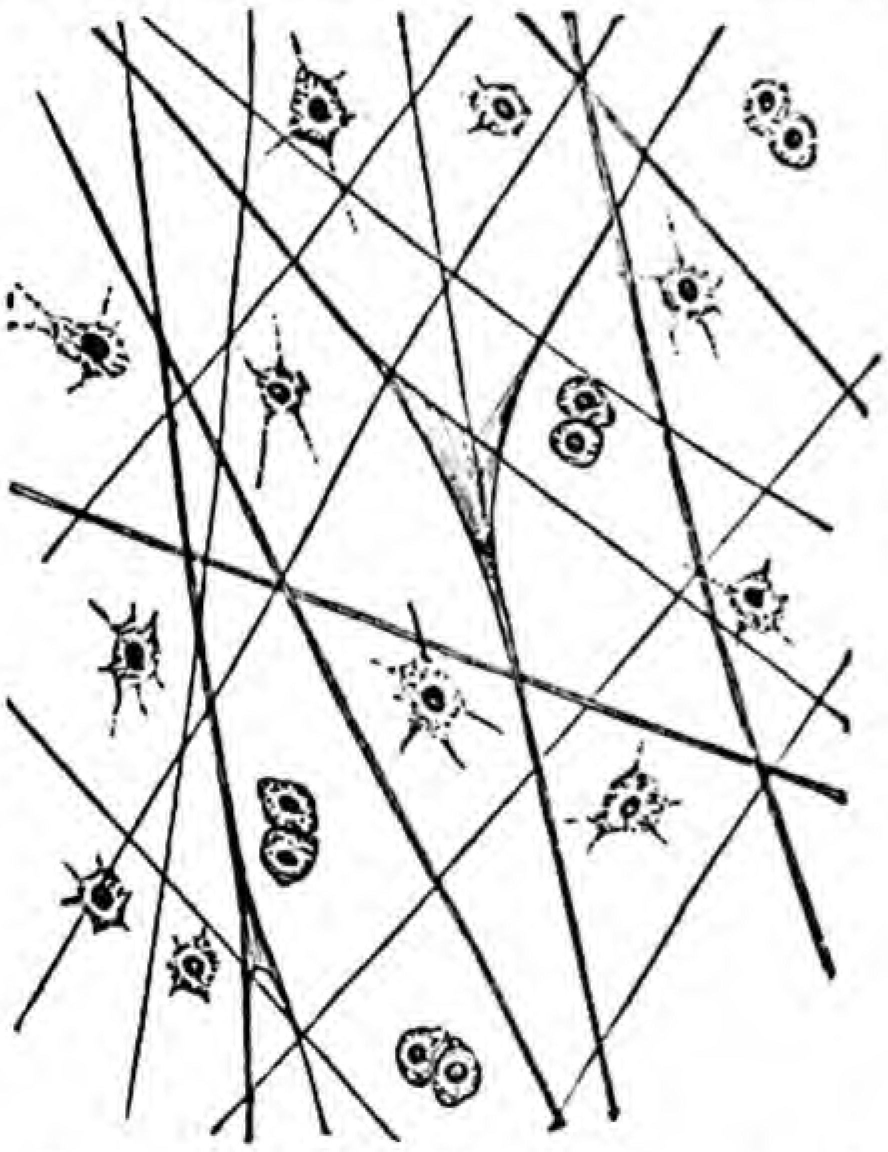


FIG. 15.—Gelatinous connective tissue of a jelly fish. (From Claus, Grobben, and Kühn's *Lehrbuch der Zoologie* (Julius Springer).)

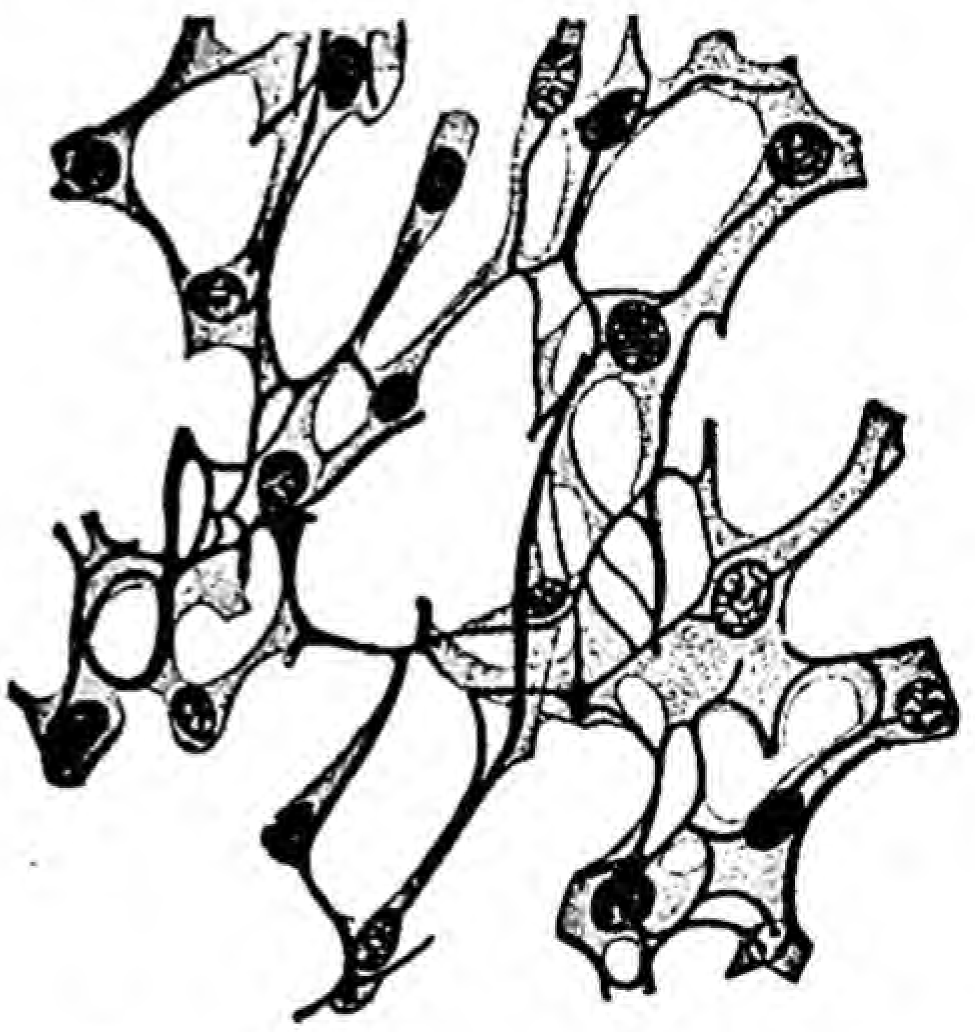


FIG. 16.—Reticular connective tissue (after Heidenhain). (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer).)

which are prolonged into fibres—the fibres from neighbouring cells joining so as to form a network. There is no true ground-substance—the inter-spaces between the cells being filled with other tissue elements.

Fibrous connective tissue, which is a very common form, has a ground-substance yielding gelatin, consisting mainly of numerous fibres, usually arranged in bundles. Thicker yellow elastic fibres may be present among the

others, and may be so numerous as to give the entire tissue an elastic character. Associated with fibrous tissue, and produced by modification of its cells, is *adipose* or *fatty tissue* (Fig. 17), which consists of masses of large cells in which the protoplasm has more or less completely become replaced by fat, the cells being bound together into groups and masses or *lobules* by means of fibrous connective tissue.

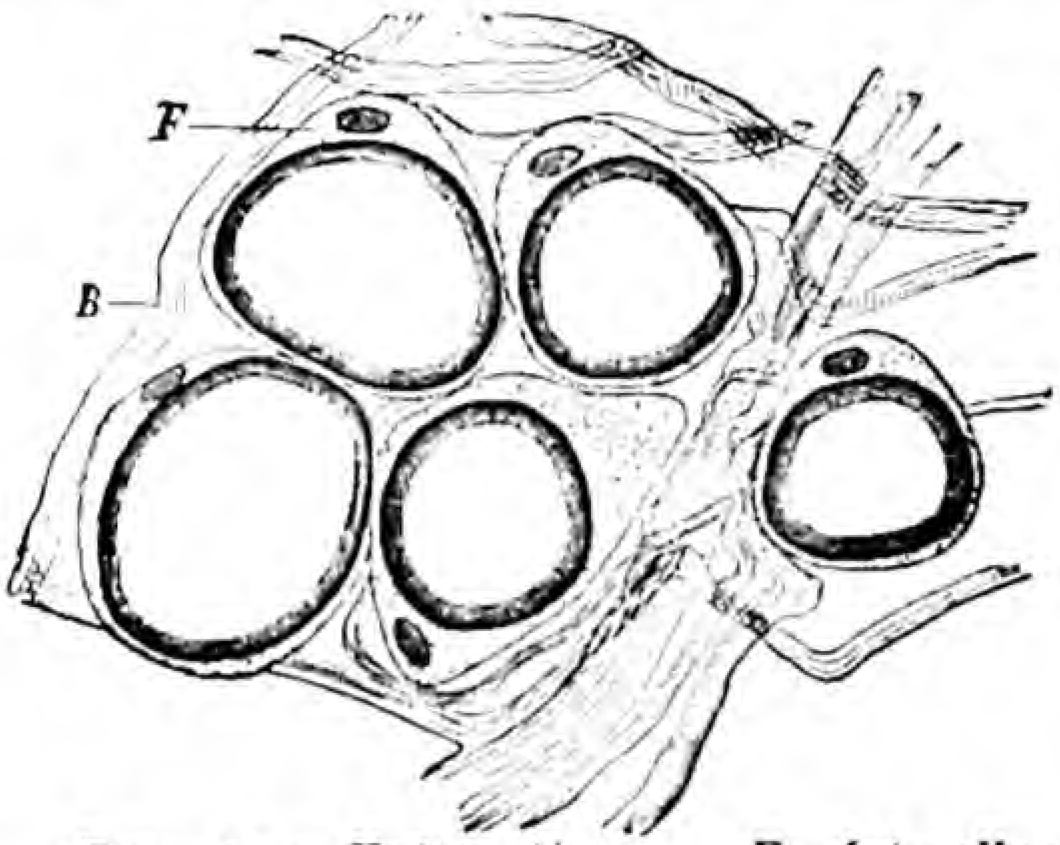


FIG. 17.—Fatty tissue. *F*, fat-cells; *B*, connective-tissue fibrils. (From Lang, after Ranvier.)

In the case of *cartilage* the matrix is of a firm but elastic character, sometimes quite homogeneous in appearance (*hyaline cartilage*, Fig. 18), sometimes permeated by systems of fibres (*fibro-cartilage*, Fig. 19), which may be of an elastic nature (*yellow elastic cartilage*). The cells are usually rounded, and as a rule several occur together in spaces scattered through the matrix; sometimes condensation of the matrix round each of the spaces in which the cells are contained forms a cell-capsule. The outer surface is covered over by a fibrous membrane—the *perichondrium*. Cartilage is frequently hardened by the deposition in the matrix of salts of lime, and is then known as *calcified cartilage*.

In *bone* (Fig. 20) the matrix is exceedingly dense and hard owing to its being strongly impregnated with carbonate and phosphate of lime. It consists typically of numerous thin lamellæ, which are arranged partly parallel with the surface, partly concentrically around certain canals—the *Haversian canals* (*c.*)—which contain blood-vessels. The cells, or *bone-corpuscles*, lie in minute spaces—the *lacunæ*—between the lamellæ, and a system of exceedingly fine channels—the *canaliculi*—extend from lacuna to lacuna, containing fine protoplasmic processes by means of which neighbouring cells are placed in communication with one another. The outer surface of the bone is covered by a vascular fibrous membrane—the *periosteum*—which takes an active part in its growth and nutrition.

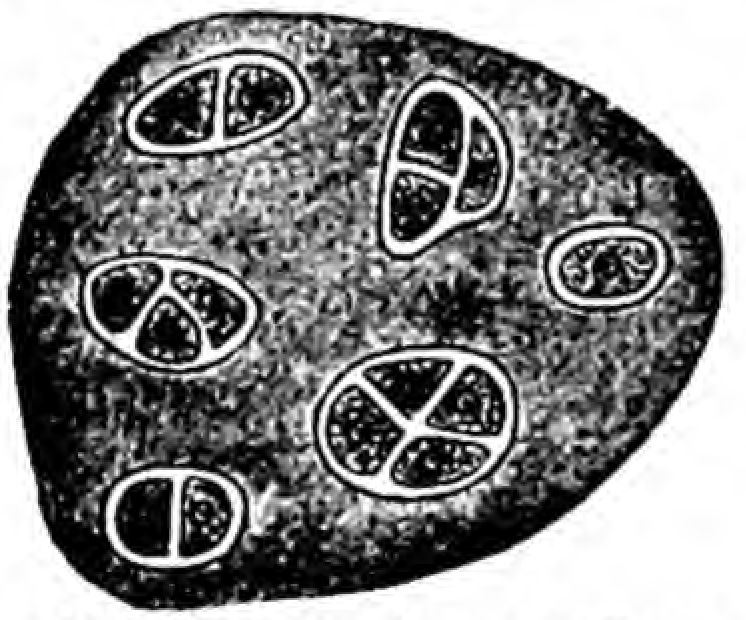


FIG. 18.—Hyaline cartilage.

FIG. 19.—Fibro-cartilage.

Highly specialized cells of the connective-tissue type are the *chromatophores* (Fig. 21). They generally have irregular cytoplasmic processes and contain *pigment—i.e.*, colouring-matter in the form of minute granules. Animal coloration is to a great extent due to the presence of such pigment-cells in the skin. Changes in the distribution of the pigment-granules within the chromatophores are responsible for the various phenomena of adaptive colour-change which is of great importance in the protective coloration of animals.

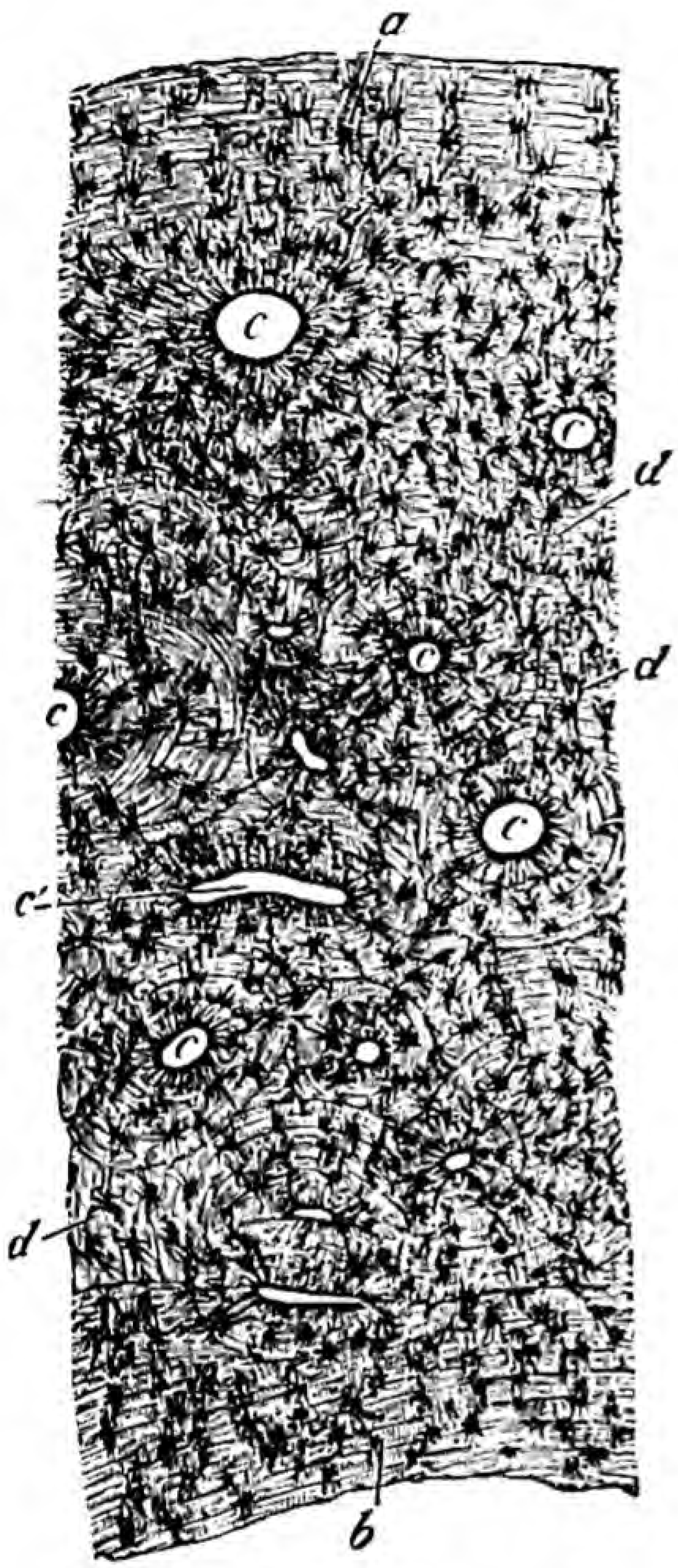


FIG. 20.—Transverse section of compact bone. *a*, lamellæ concentric with the outer surface; *b*, lamellæ concentric with the surface of the marrow cavity; *c*, sections of Haversian canals; *c'*, section of a Haversian canal just dividing into two; *d*, interstitial lamellæ. (From Huxley's *Lessons in Physiology*.)

The tissues just described are generally more or less passive in the functions which they perform, serving mainly for support and for binding together the various organs. **Muscular tissue,** on the other hand, has an active part to play—this being the tissue by means of which, in general, all the *movements* of the body of an animal are brought about. Muscular tissue varies greatly in minute structure in different groups of animals, and even in different parts of the same animal. It consists of microscopic fibres aggregated together into large bundles or layers. These fibres are composed of a substance—the *muscle-substance*—which consists of numerous fine fibrils, so-called *myofibrils*, and which when living has the special property of *contractility*, contracting or becoming shorter and thicker on the application of a *stimulus*. There are two

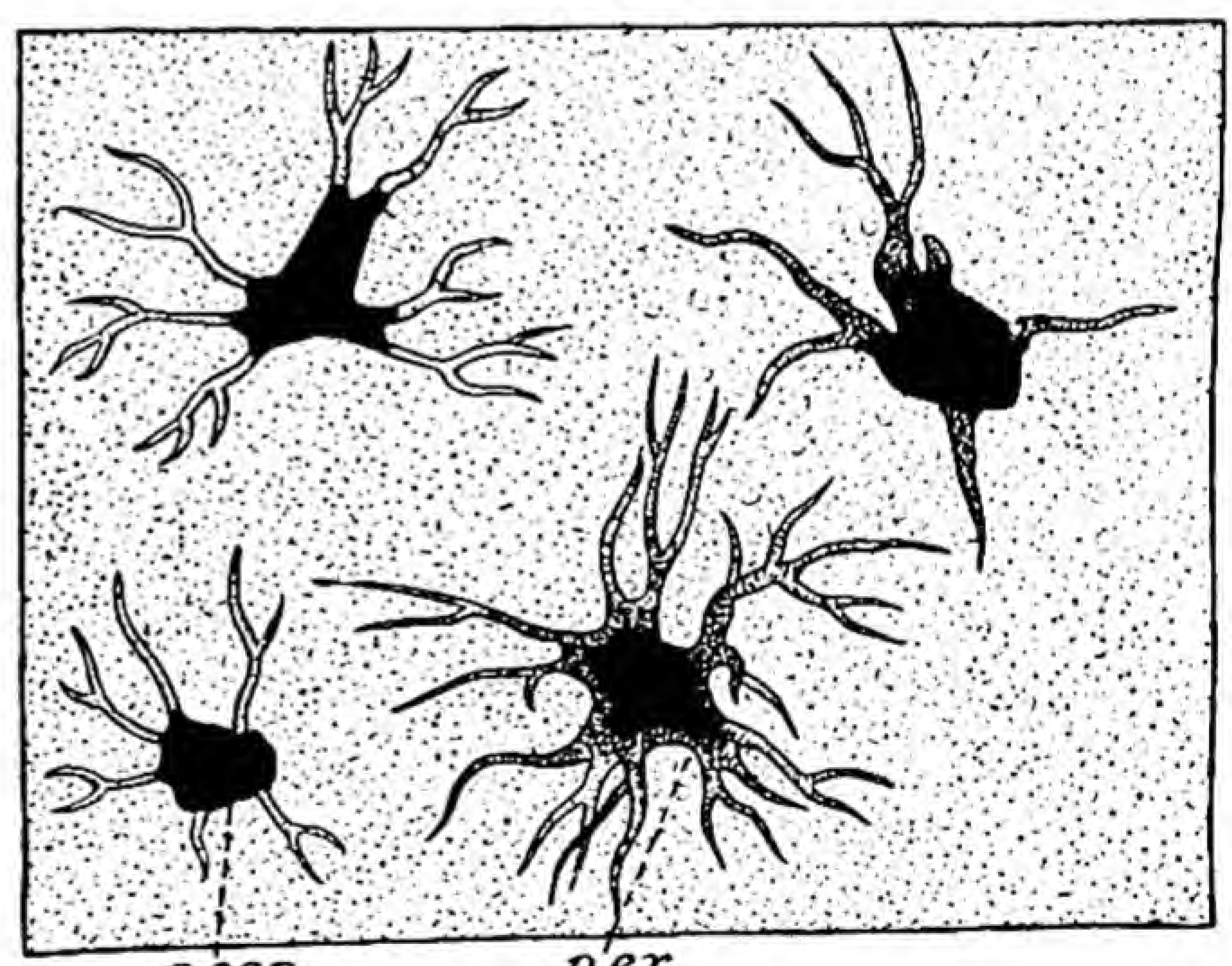


FIG. 21.—Chromatophores in the skin of the frog. *p. con.* pigment contracted; *p. ex.* pigment expanded. (From Borradaile's *Manual of Elementary Zoology* (Oxford University Press).)

principal varieties of muscular tissue to be distinguished, termed respectively *unstriated* or *smooth*, and *striated* muscle. Each fibre of smooth muscle (Fig. 22A) is usually a single, greatly elongated cell, sometimes branched, with a single nucleus; it may contain a core of unaltered protoplasm, or all except the nucleus may be altered into fibrils of muscle-substance; cross-striation is absent. A fibre of striated muscular tissue (Fig. 22B) is formed by the close union of several cells which are represented by their nuclei. Sometimes there is a core of protoplasm; but more usually the entire fibre is composed of fibrillar muscle-substance, with perhaps a remnant of protoplasm in the neighbourhood of each nucleus. The substance of the fibre is crossed by numerous transverse bands and striæ, the precise significance of which is a matter of controversy. The fibre is usually enclosed in a delicate sheath—the *sarcolemma*. Striated muscular tissue is specially characteristic of parts in which rapid movement is necessary. A special type of striated muscle is the *heart-muscle* of vertebrate animals. Its fibres are branched and form a network.

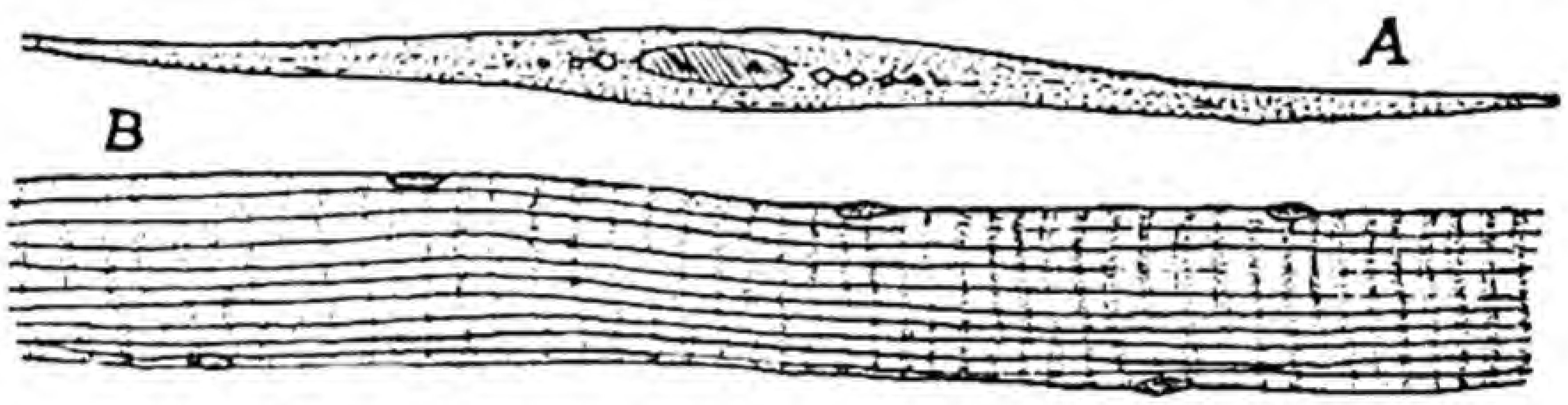


FIG. 22.—*A*, unstriated (smooth) muscle cell with single nucleus; *B*, shows a small portion of the length of a multinucleate striated fibre. (From Kingsley's *Comparative Anatomy of Vertebrates* (Copyright P. Blakiston's Son & Co., Inc., Publishers).)

Muscular action frequently takes place in response to stimuli imparted upon the animal from outside, and its efficiency largely depends on complete co-ordination of the movement of different groups of muscles. The conducting of the effect of stimulation from the sensory receptor-cells to the muscles, and the co-ordination of muscular activity are mainly carried out by the **nervous-tissue.** The principal element of the nervous-tissue is the *neuron* (Fig. 23). It consists of a relatively large nerve-cell (*nc.*) with a large nucleus and several processes. One of these processes is usually much longer than the rest, and represents what is called a *nerve-fibre* (*nf.*). The essential part of the nerve-fibre is a continuous strand of protoplasm produced from the nerve-cell and known as the *axon* or *axis-cylinder* (*a.*). This is made up of fine fibrillæ or *neuro-fibrils* embedded in a more fluid material. They are supposed to be continuous throughout the nerve-cell and its processes, and to represent the conducting element of the nerve-fibre. In higher animals the most characteristic form is the *medullated* nerve-fibre. In this the axis-cylinder is surrounded by a layer of white glistening material, known as *myelin*, forming the *medullary sheath* (*ms.*). This is enclosed in turn in a very delicate, structureless membrane, the *neurolemma* (*nl.*). At fairly regular intervals a break occurs in the medul-

lary sheath, the neurolemma coming into close relation with the axis-cylinder. The interruptions in the medullary sheath are known as *nodes of Ranvier*. Another kind of nerve-fibres, the *non-medullated* fibres, differ from the medullated fibres simply by the absence of the medullary sheath. Numerous nerve-fibres are usually united into bundles surrounded by a connective-tissue sheath called *perineurium*. Several or many of such bundles unite to form a *nerve*, which is enwrapped in a relatively thick sheath of connective tissue, the *epineurium*.

The blood, the lymph, and other similar fluids in the body of an animal may be looked upon as **liquid tissues,** having certain cells—the *corpuscles*—disseminated through a liquid *plasma*, which takes the place of the ground-substance of the connective tissues. In a large proportion of cases such corpuscles are similar to Amœbæ in their form and movements (*amœboid corpuscles, leucocytes*). In the blood of Vertebrates leucocytes occur along with coloured corpuscles (*erythrocytes*) of definite shape

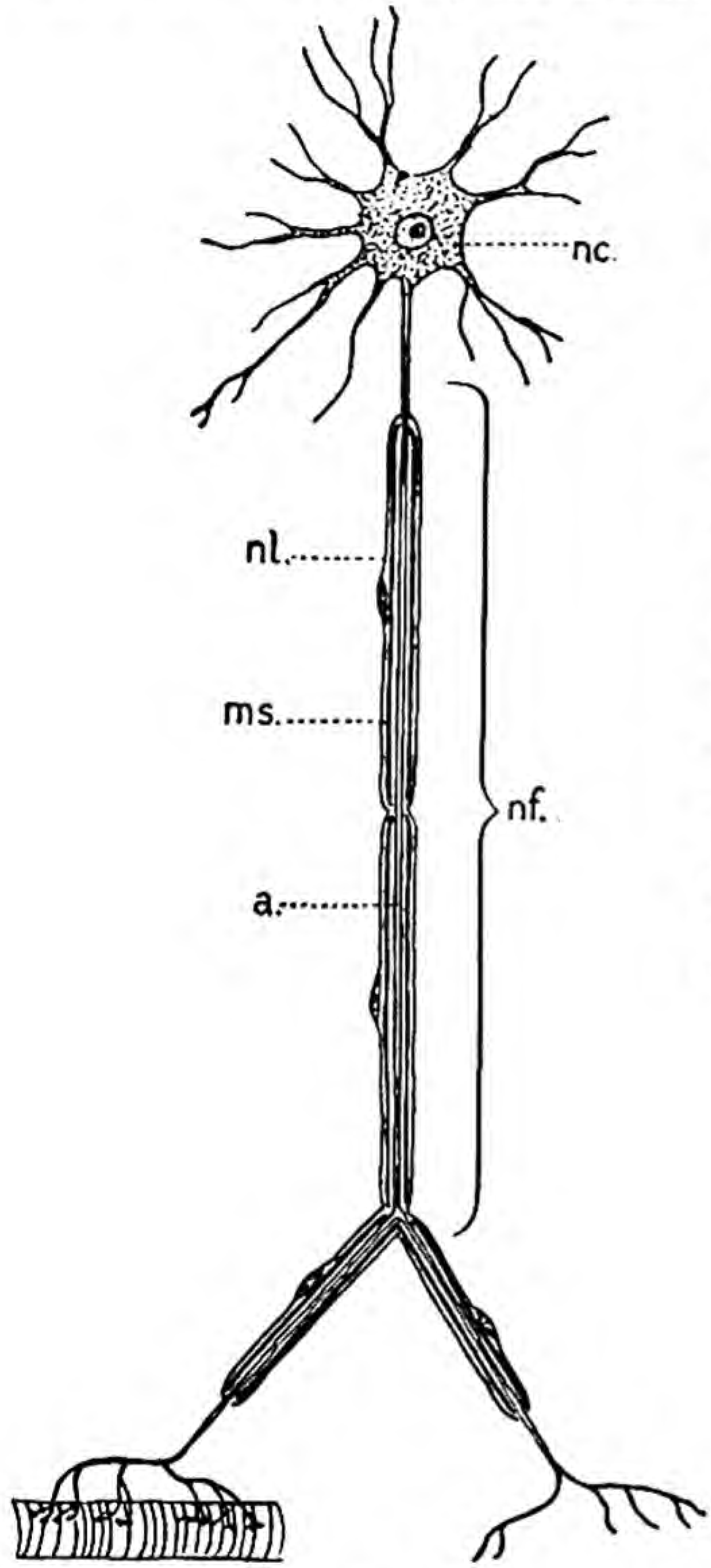


FIG. 23.—Diagram of a neuron. *a.* axon; *ms.* medullary sheath; *nc.* nerve-cell; *nf.* nerve-fibre; *nl.* neurolemma. (After Claus, Grobben, and Kühn's *Lehrbuch der Zoologie* (Julius Springer).)

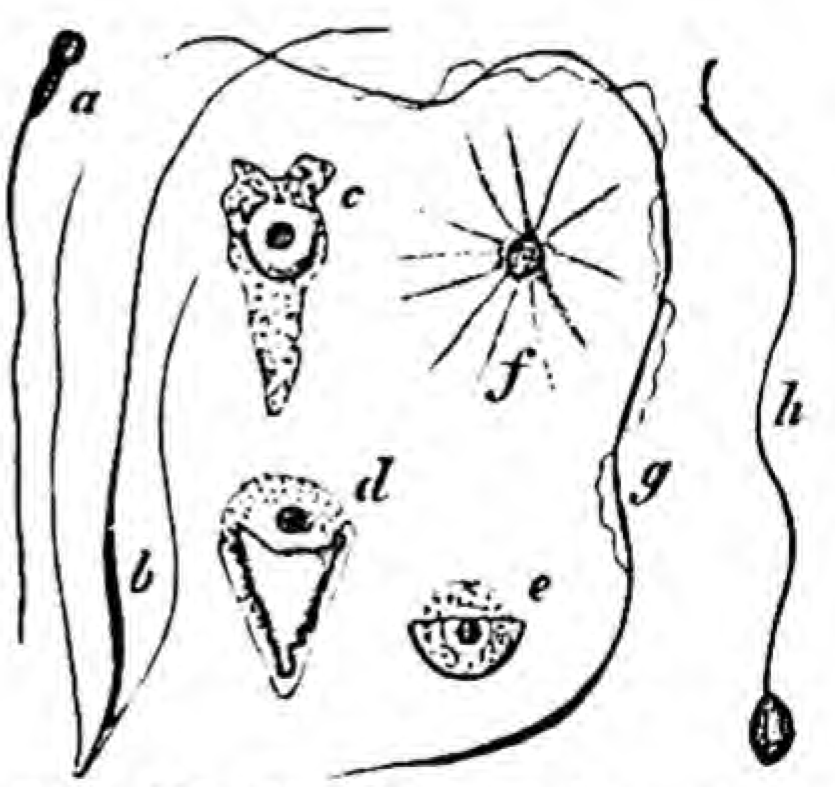


FIG. 24.—Various forms of spermatozoa. *a* of a Mammal; *b*, of a Turbellarian worm; *c*, *d*, and *e*, of Nematode worms; *f*, of a Crustacean; *g*, of a Salamander; *h*, the commonest form with oval head and long flagellum. (From Lang's *Comparative Anatomy*.)

containing the red-colouring matter (*hæmoglobin*) of the blood. The leucocytes are able, like Amœbæ, to ingest solid particles.

The **reproductive tissues** generally consist of so-called *primordial germ-cells*, which are frequently scattered among indifferent cells of the connective-tissue type. From the primordial germ-cells ova or spermatozoa take their origin (Figs. 7, 9, and 24).

5. Organs.

The chief systems of organs of an animal are the *integumentary*, the ***skeletal***, the *muscular*, the *nervous* and the *sensory*, the ***alimentary*** or ***digestive***, the *vascular*, the *respiratory*, the *excretory*, and the *reproductive*.

In the majority of animals the **skin** or **integument** (Fig. 25) consists of a cellular membrane, the *epidermis* (*ep.*), and of a fibrous layer, the *dermis* (*derm.*), situated below it. The epidermis may consist of one layer or may be stratified. In many animals it is covered by a non-cellular *cuticle*. This is a product of secretion of the cells of the epidermis. The cuticle is sometimes very thin

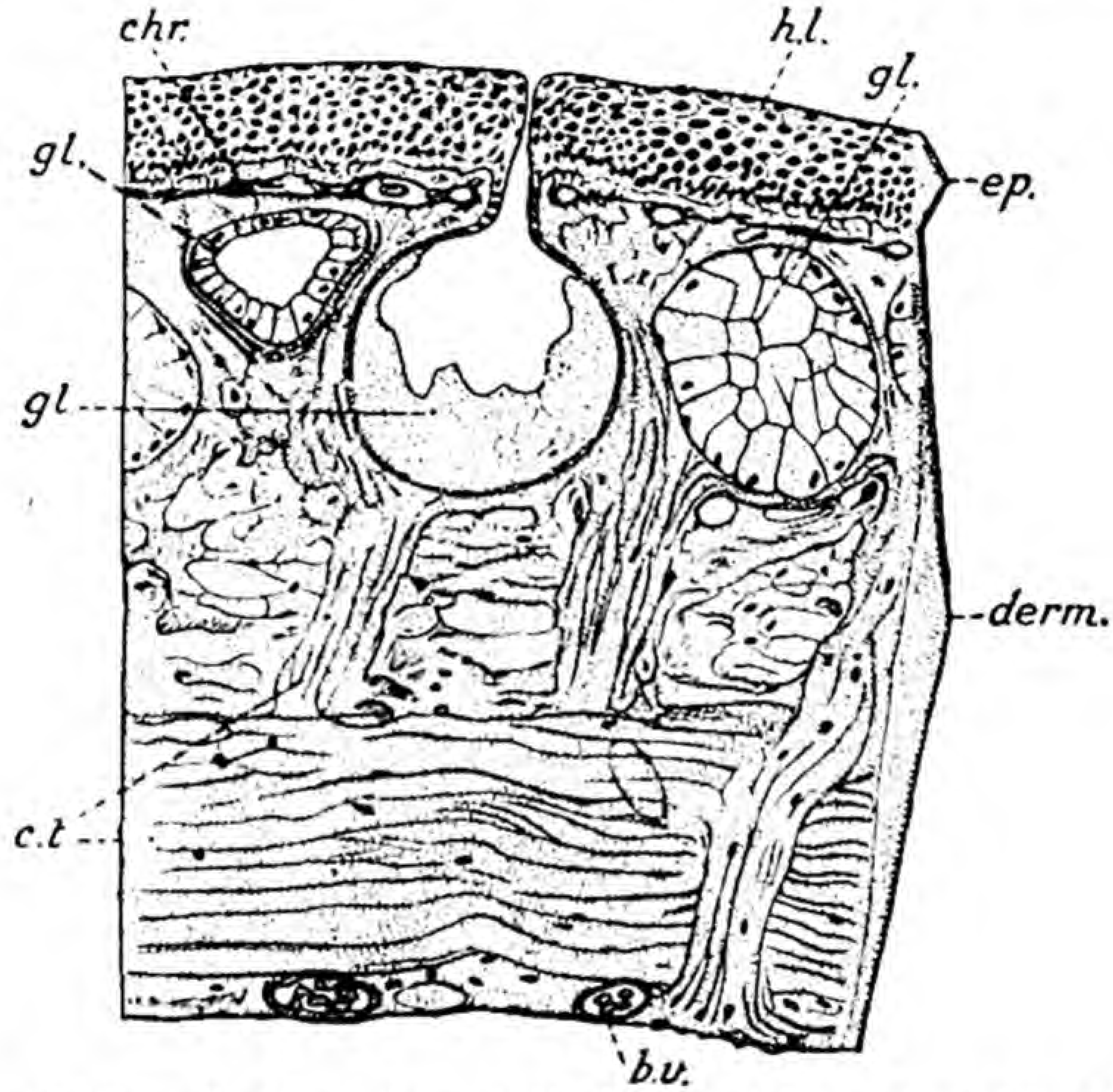


Fig. 25.—Skin of frog. Section taken vertically to surface: *b. v.* blood vessels; *chr.* layer of chromatophores; *c. t.* layers and strands of connective tissue; *derm.* dermis; *ep.* epidermis; *gl.* mucus gland; *h. l.* horny layer of the epidermis. (From Borradaile's *Manual of Elementary Zoology* (Oxford University Press).)

and delicate; in many animals it becomes greatly thickened and hardened, so as to form a strong, protective crust, either of a material termed ***chitin***, which is somewhat akin to horn in its consistency, or solidified by deposition of calcareous salts. In cases where the epidermis is stratified, the upper layers of cells may be altered into *horn* (*h.l.*), the cuticle being absent. Hard parts formed by the dermis are *bone* and other skeletal structures of calcareous nature.

Hairs and *feathers* are horny formations taking their origin from the epidermis. Their chief function is to help in keeping the body temperature of warm-blooded animals constant. Temperature regulation in many warm-

blooded animals is supported by the evaporation of fluid secreted by *sweat-glands*, which are situated in the dermis opening upon the body-surface by means of a duct. In many animals the body-surface is kept moist and slippery by the secretion of *mucus-glands* (*gl.*), in others it is kept greasy by the fatty secretion of so-called *sebaceous glands*. Milk-secreting *mammary glands*, *wax glands* and *spinning glands* are other examples of glands to be found in the integument of animals.

Owing to the presence of various sensory elements—*e.g.*, *sensory cells* or free endings of *nerve-cells*, the epidermis represents a highly sensitive surface by means of which changes going on in the environment are continuously communicated to the organism. The skin is thus a highly important organ which, apart from its protecting and supporting function, helps in adjusting the vital processes within the animal to the continuous changes in external conditions.

The term **skeleton** or **skeletal system** is applied to a system of hard parts, external or internal, which serves for the protection and support of softer organs and often for the attachment of muscles. This system of hard parts may be external, enclosing the soft parts, or it may lie deep within the latter, covered by integument and muscles; in the former case it is termed an *exo-skeleton* or *external skeleton*; in the latter an *endoskeleton* or *internal skeleton*.

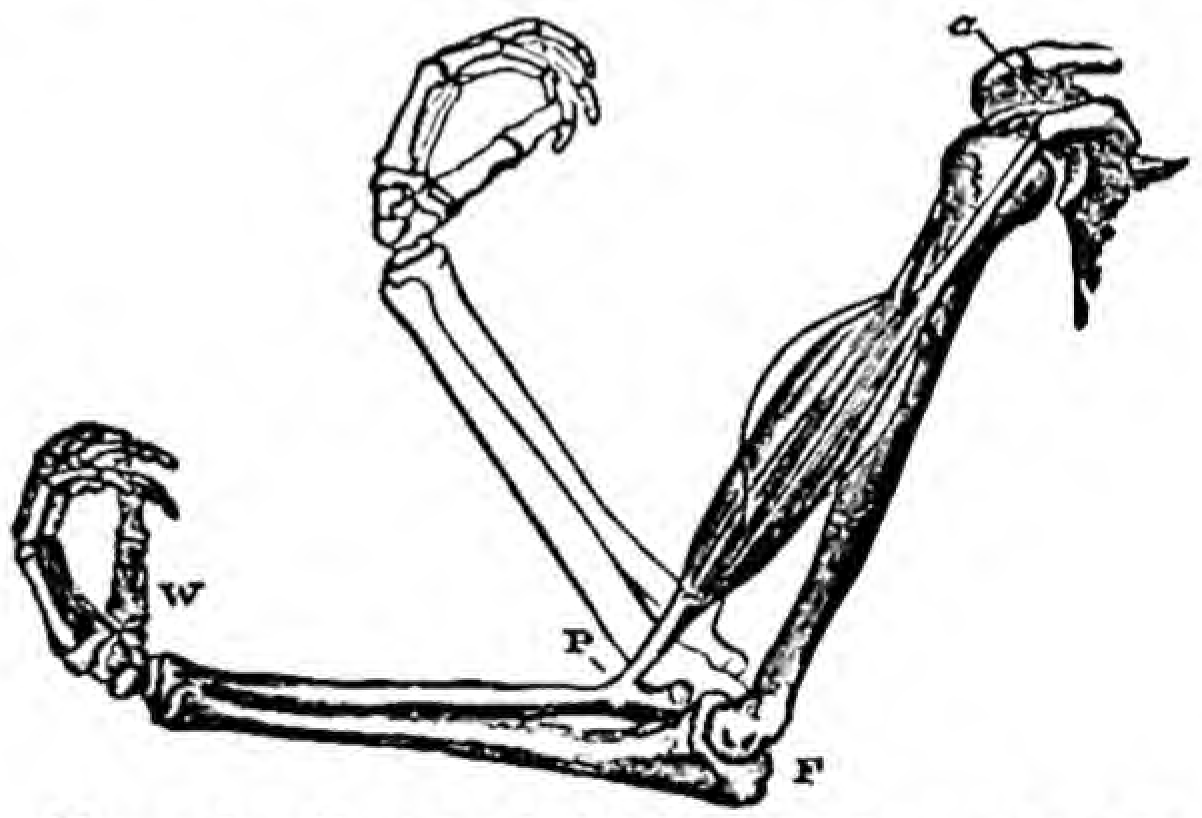


FIG. 26.—Bones of the human arm and fore-arm with the biceps muscle, showing the shortening and thickening of the muscle during contraction and the consequent change in the relative position of the bones—viz., flexion of the fore-arm on the upper arm. (From Huxley's *Physiology*.)

In many groups of animals both systems are developed. An *exoskeleton* is formed by the thickening and hardening of a part or the whole of one of the layers of the integument enumerated above; or more than one of these layers may take part in its formation. In many invertebrate animals, such as Insects, Crustaceans, and Molluscs, it is a greatly thickened and hardened cuticle which forms the exoskeleton. The horny scales of Reptiles are examples of an exoskeleton derived from the epidermis, while the bony part of the shell of Turtles and the bony scales of Fishes are examples of a dermal exoskeleton.

When an *endoskeleton* is present, it usually consists either of cartilage or bone or of both; but sometimes it is composed of numerous minute bodies (*spicules*) of carbonate of lime or of a siliceous material.

A skeleton, whether internal or external, is usually composed of a number of pieces which are movably articulated together, and which thus constitute a system of jointed levers on which the muscles act.

A **muscle** is a band or sheet of muscle-fibres endowed in the living state with the property of *contractility*, by virtue of which, when stimulated in certain ways, it contracts in the direction of its length, becoming shortened, and at the same time thickened (Fig. 26). The extremities of the muscle are frequently composed of a form of strong fibrous connective tissue—the *tendon* of the muscle. The ends of the muscle are usually firmly attached to two different parts of the jointed framework or skeleton, external or internal; and, when the muscle contracts and becomes shortened, these two parts are drawn nearer to one another.

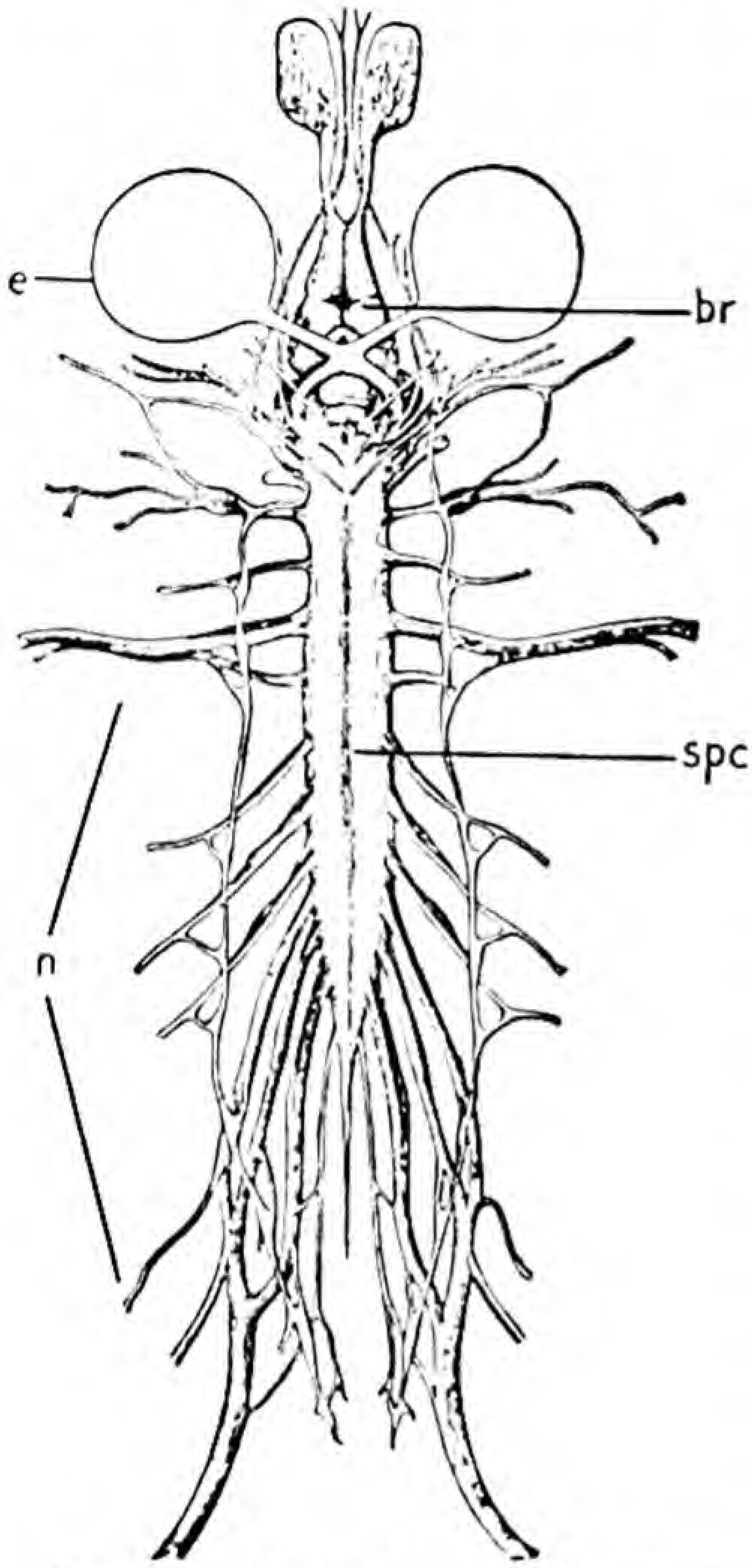


FIG. 27.—Ventral view of the nervous system of the frog. *br.* brain; *e.* eye; *n.* nerves; *sp. c.* spinal cord. Brain and spinal cord together make up the central nervous system. (From Woodruff's *Animal Biology* (Macmillan Co.) after Ecker.)

In many cases muscles are not attached to any skeletal structure, but are arranged in layers around a body-cavity, the layers differing from one another in their direction of contraction. Muscular arrangements of this kind serve in the locomotion of worm-like animals and in the transport of substances through hollow organs, such as the gut or the blood-system.

In all but the most lowly-organised animals there is a **nervous system** by means of which a communication is effected between the various parts of the body, enabling them to work in harmony, and by means of which also a communication is established between the organism and the external world. In the most primitive case the nervous system consists of a network of neurons distributed all over the body. The processes of these neurons are connected with each other as well as with sensory cells and effector organs such as muscles or glands. This type of nervous system is called *nerve-net* (Fig. 111, p. 142).

In the more highly organized state the cell-bodies of a large number of neurons aggregate into masses of nervous matter, called *ganglia*. These ganglia represent the central part of the nervous system, which in the most highly organized animals, the vertebrates, takes the form of a *brain* situated in the head and a *spinal cord* running along the back of the animal (Fig. 27).

The nerve-fibres taking their origin from the central nervous system and connecting it with the various organs of the body are usually assembled into nerves, which form the *peripheral* part of the nervous system. Messages in the form of wave-like electrical disturbances (*nervous impulses*) are conveyed to the central parts along *afferent* nerve-fibres. Similar nervous impulses leave the central nervous system and are conveyed along *efferent* nerve-fibres to the various organs of the body, causing these to become active, or governing their activity.

The function of the central nervous system is to co-ordinate the responses to the various external and internal stimuli. Such responses, if they are of

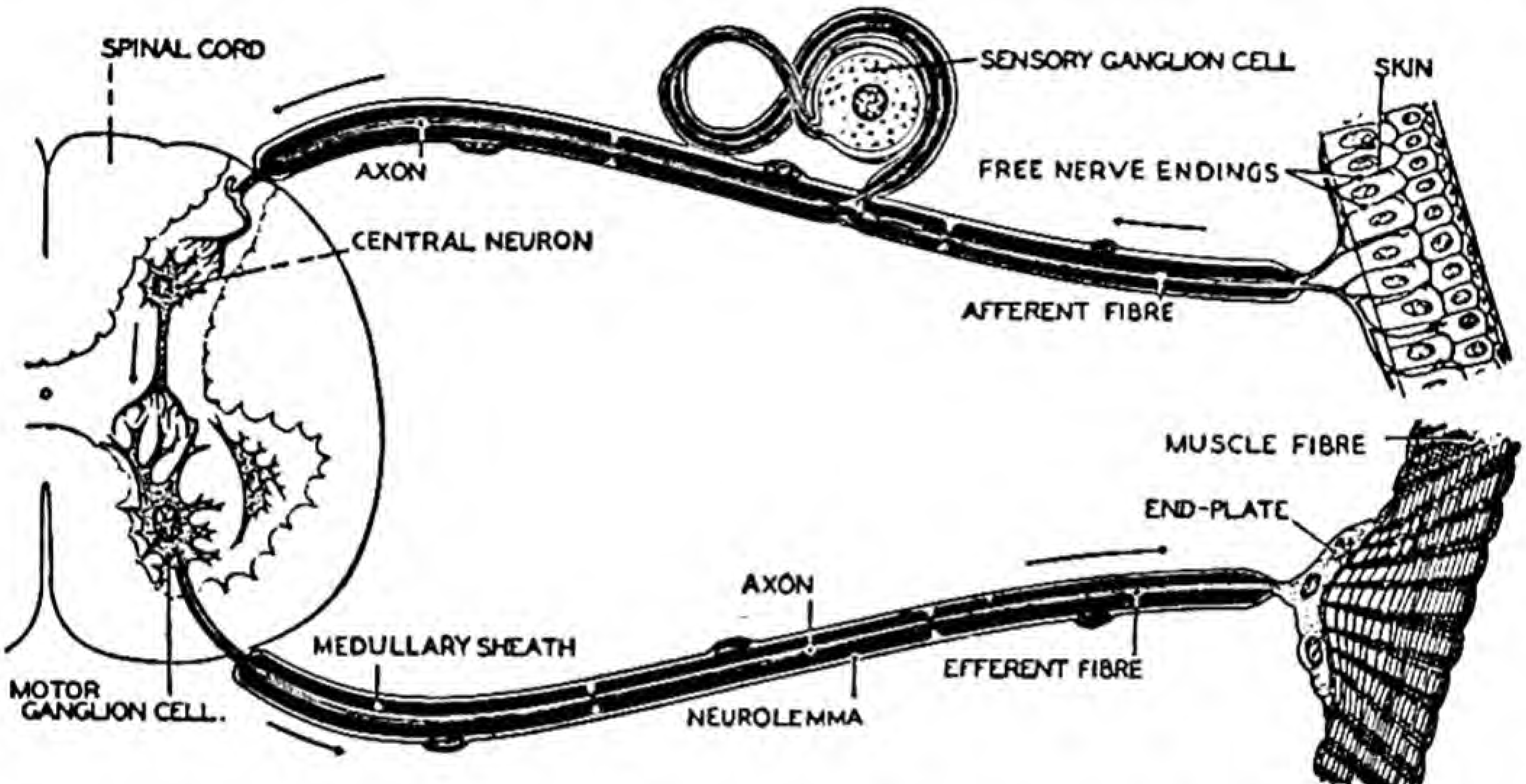


FIG. 28.—Diagram of a reflex-arc. Three neurons—afferent, central, and efferent—are shown in their relations to one another and to the skin and muscle. The central neuron is located in the grey matter of the spinal cord. (From Neal and Rand's *Comparative Anatomy* (Copyright P. Blakiston's Son & Co., Inc., Publishers).)

a simple type, are usually called *reflexes*. The structures concerned in reflex activity—*sense-organs, afferent neurons, central neurons, efferent neurons, effector organs* (muscles and glands)—form together so-called *reflex-arcs* (Fig. 28).

It has been pointed out above that in many animals the whole of the integument serves as one large sense-organ, receiving external stimuli and handing them on to the rest of the body. This irritability is due mainly to the presence in the integument of various sensory elements, amongst which three main types have to be distinguished (Fig. 29).

In the simplest, yet perhaps not the most primitive, case we find free ramifications of a *sensory neuron* extending into the integumentary epithelium, where they are distributed amongst the ordinary epithelial cells. Such *free nerve terminations* (Fig. 29, *a*.) are held to be responsible for the reception of certain types of mechanical stimulation, for the sensitivity to warmth and cold, and they may perhaps be considered to be the origin of the sensation of pain.

In contrast to the sensory neurons, whose cell-bodies are generally found in a subepithelial position, the cell-bodies of the *neurosensory cells* (Fig. 29, *b.*) and of the *secondary sensory cells* (Fig. 29, *c.*) are situated in the epithelium side by side with ordinary epithelial cells. The former, which are also called *primary sensory cells*, possess a nervous process by means of which they make connection either with the neurons of a nervous ganglion or directly with an underlying effector organ. The secondary sensory cells have no such conducting processes of their own. They are epithelial cells which, on being stimulated, hand the stimulus on to the peripheral ramifications of a sensory neuron with which they are in close contact.

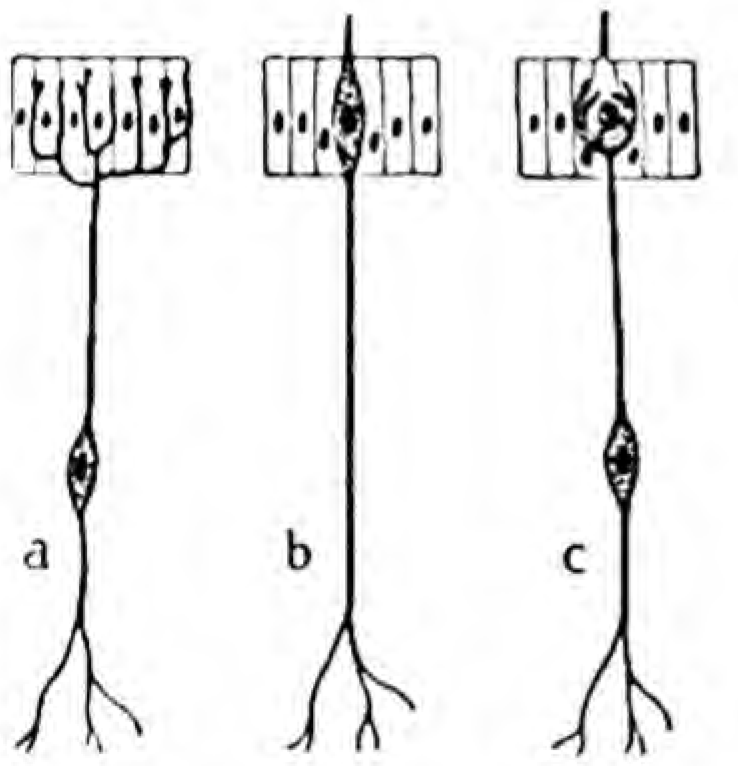


FIG. 29.—Three types of sensory elements. *a*, sensory neuron with free nerve terminations; *b*, neurosensory cell; *c*, secondary sensory cell with neuron. (Modified after Kühn's *Grundriss der Allgemeinen Zoologie 5. Auflage* (Verlag Georg Thieme, Leipzig, 1936).)

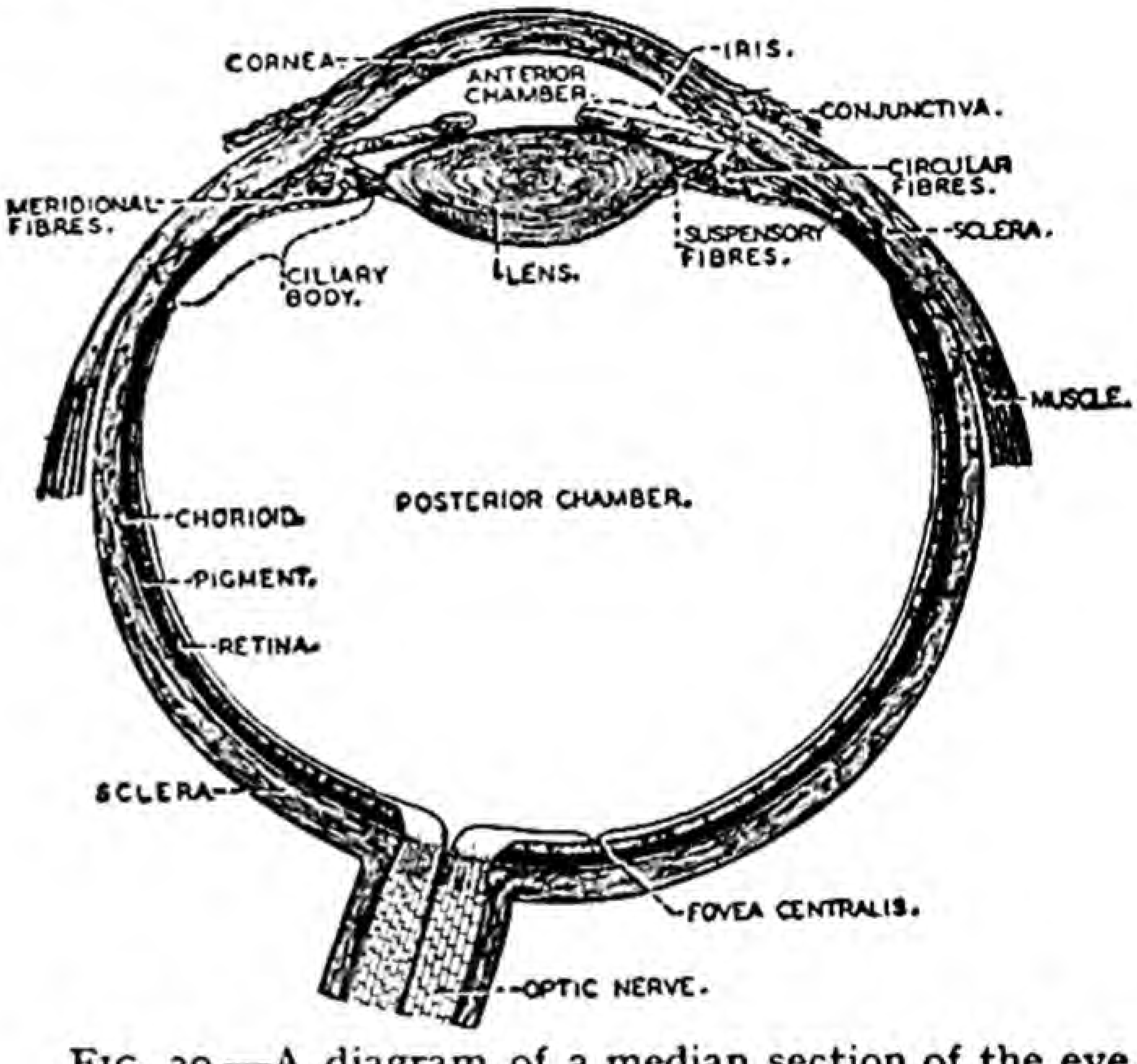


FIG. 30.—A diagram of a median section of the eye. (After Sobotta's *Anatomy* (W. B. Saunders Co.).)

Neurosensory cells and secondary sensory cells are found to be the sensitive elements of the more highly specialized sensory structures, the **sense-organs.** Thus, the photosensitive cells in the *retina* of the vertebrate *eye* and the *olfactory* receptor cells situated in the epithelium coating the cavities of the vertebrate *nose* have the structure of neurosensory cells; the sensory elements in the vertebrate ear and the *gustatory* receptor cells found in the so-called *taste-buds* of the *tongue* are secondary sensory cells. In many cases *auxiliary* structures are added to the sensory elements; their function is to increase the efficiency of the sense-organ. Thus, in the case of the highly developed vertebrate eye (Fig. 30), the light-sensitive sensory elements are arranged in a very thin layer, the retina, coating the interior wall of the eye-ball. The cornea, the iris, and a highly refractive lens together with a system of muscles contained in the ciliary body form an auxiliary apparatus which serves in focussing the light-rays on the retina. A pigment-screen absorbs the light-rays and prevents their

passage beyond the retina. The whole organ is supported and protected by a tough layer of fibrous tissue, the sclera, in which it is enclosed.

The **alimentary** or **digestive system** consists of a cavity or system of cavities into which the food is received, in which it is digested, and through the wall of which the nutrient matters are absorbed. As a rule a series of glandular organs communicate with the digestive cavities by means of a duct.

In the lowest groups in which a distinct *alimentary* or *enteric cavity* is present it is not distinct from the general cavity of the body; but in all higher forms there is an *enteric canal* which is suspended within the cavity of the body, and the lumen of which is completely shut off from the latter. It may have simply the form of a sac or bag with a single opening which serves both as *mouth* and *anus*; in other cases the sac becomes branched and may take the form of a system of branching canals. In most animals, however, the alimentary canal has the form of a longer or shorter tube beginning at the mouth and ending at the anal opening. In most cases there are organs in the neighbourhood of the mouth serving for the seizure of food; these may be simply *tentacles* or soft, finger-like appendages, or they may have the form of *jaws*, by means of which the food is not only seized, but torn to pieces or pounded up to small fragments in the process of mastication.

In general there may be said to be three regions in the alimentary canal—the *ingestive*, the *digestive* and *absorbent*, and the *egestive* or *efferent*. The *ingestive* region is the part following behind the mouth, by which the food reaches the digestive and absorbent region. But, besides serving as a passage, it may also act as a region in which the food undergoes certain changes, chiefly mechanical, which prepare it for digestion. This ingestive region may comprise a *mouth-cavity* or *buccal cavity*, a *pharynx*, an *œsophagus* or *gullet*, with sometimes a muscular *gizzard* which may be provided with a system of teeth for the further breaking up of the food, and sometimes a *crop* or food-pouch. On passing through the ingestive region the food may be mixed with the secretion of *salivary glands*, making the food-lump slippery and, in many cases, altering its chemical composition (*vide infra*).

The *digestive* and *absorbent* region is the part in which the chemical processes of digestion go on, and from which takes place the absorption of the digested food-substances. Into this part are poured the secretions of the various *digestive glands*, which act on the different ingredients of the food so as to render them soluble. This region may present a number of subdivisions; nearly always there are at least two—a wide sac, the *stomach*, mainly digestive in function, and a narrow tube, the *intestine*, in which both digestion and absorption take place. Through the lining membrane of the intestine the digested nutrient matter passes either into the body-cavity around the alimentary canal, or into the channels of a vascular system.

The *egestive* or *efferent* region of the alimentary canal is the posterior part

of the intestine, in which digestion and absorption do not go on, or only go on to a limited extent, and which serves mainly for the passage to the anal opening of the *fæces* or unabsorbed constituents of the food.

The whole of the interior of the alimentary canal is lined by a layer of cells—the *alimentary* or *enteric epithelium*. The form and arrangement of the cells of this epithelium vary greatly in different groups of animals. In some lower forms, the cells lining the alimentary cavity have the power, like Amœba, of thrusting forth processes of their protoplasm and of taking minute particles of food into their interior to become digested and absorbed (*intracellular digestion*). Sometimes they are all more or less active in secreting a fluid

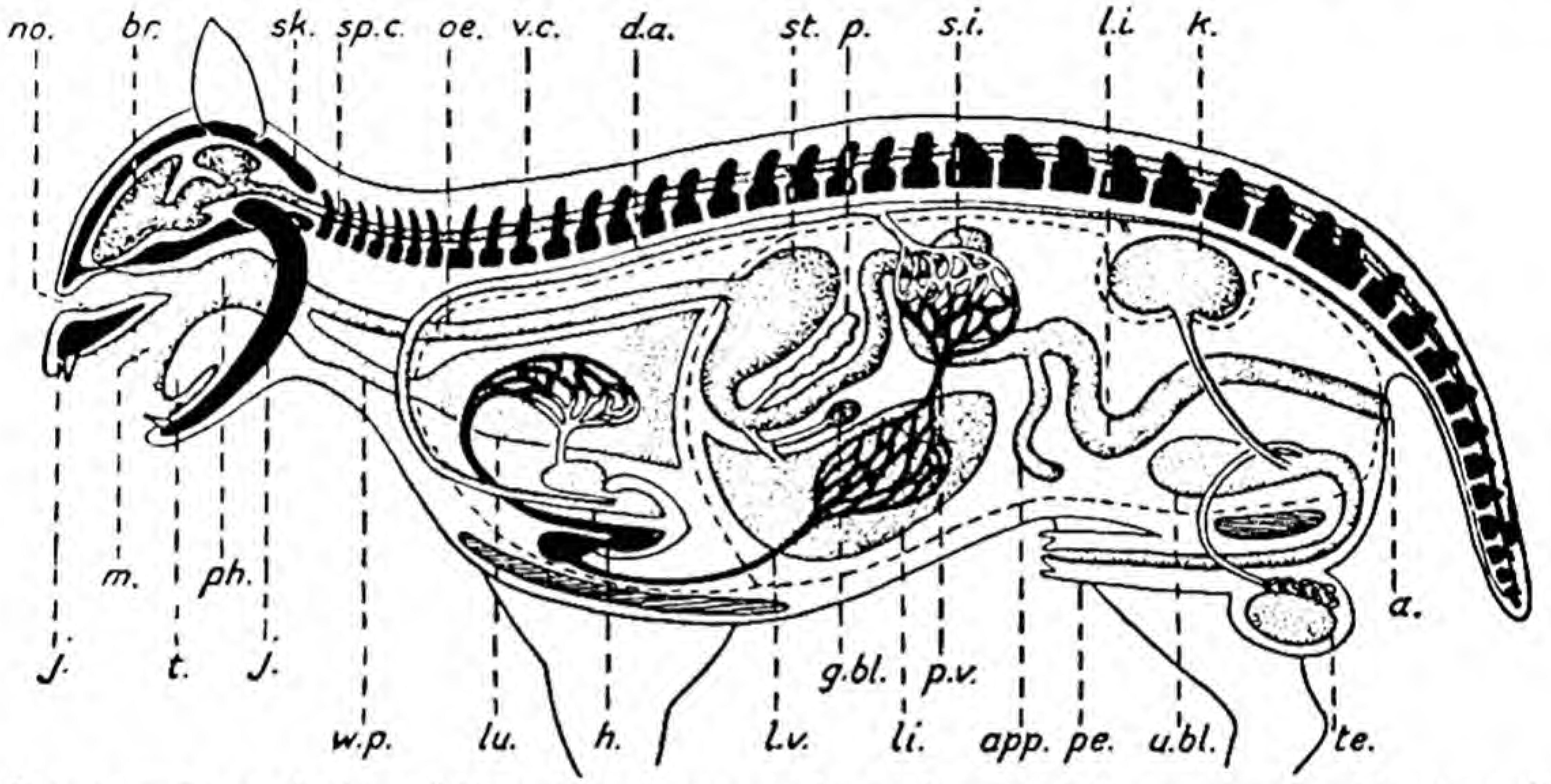


FIG. 31.—General view of the internal organs of a male mammal. *a.* anus; *app.* appendix; *d. a.* dorsal aorta; *g. bl.* gall bladder; *h.* heart; *j.* jaw; *k.* kidney; *li.* liver; *l. i.* large intestine; *lu.* lung; *l. v.* liver vein; *m.* mouth; *no.* nose; *œ.* œsophagus; *p.* pancreas; *pe.* penis; *ph.* pharynx; *p. v.* portal vein; *s. i.* small intestine; *sk.* skull; *sp. c.* spinal cord; *st.* stomach; *t.* tongue; *te.* testis; *u. bl.* urinary bladder; *v. c.* vertebral column; *w.p.* windpipe. (After Kühn's *Grundriss der Allgemeinen Zoologie*, 5. *Auflage* (Verlag Georg Thieme, Leipzig, 1936).)

into the gut-cavity destined to act on the food and render it soluble (*extra-cellular digestion*); sometimes this function is confined to certain of the cells, which have a special form; very often the secreting cells line special little pouch-like, simple or branched *glands*, opening by a passage or *duct* into the main cavity of the alimentary canal. Besides these glands formed from specially modified cells of the enteric epithelium there are nearly always present certain large special glands, separate from the alimentary canal itself, but opening into it by means of ducts. Of these the most generally occurring are the glands termed *salivary glands*, *liver*, and *pancreas*. The *salivary glands* have the function of secreting a fluid called the *saliva*, which, in many cases at least, has a special action on starchy matters, converting them into sugar. The ducts of these glands open always, not into the digestive, but into some part of the ingestive region of the alimentary system.

The most important function of the *liver* is one distinct from the process of digestion; its secretion—the *bile*—has, however, at least a mechanical effect on this process, and assists the secretion of the pancreas in its effects upon fat. In lower forms the organ to which the term liver is commonly applied appears in many cases to combine the functions of a true liver with that of a pancreas, and is thus more appropriately termed *hepatopancreas* (liver-pancreas).

The *pancreas* secretes a fluid, the *pancreatic juice*, which plays a very important part in digestion. It usually contains a number of substances which in their chemical action can be compared with catalysers. The general term *enzymes* is applied to these substances, and their proper names usually indicate the kind of food-stuff upon which they act. Thus there is an enzyme called *amylase*, which acts upon starch (amylum), converting it into sugar. Food-substances of the nature of *proteins* are split up into substances of smaller molecular weight with the aid of *proteases*, and finally converted into soluble *amino-acids* by the action of various other enzymes. A *lipase* is active in splitting up fatty material into *glycerol* and *fatty acids*. The pancreatic juice is frequently supported by similar secretions from the epithelium of the stomach and the intestine.

When the food has been acted on by the various digestive secretions, the soluble part of it is fitted to be taken up and absorbed through the wall of the alimentary canal into the blood (in animals in which a blood-system exists), or into the fluid which takes its place. In the higher animals a part of the soluble matter of the food passes directly into the blood contained in the blood-vessels; while another part is taken up by a set of special vessels, the *lacteals*, which are a part of the lymphatic system, and reaches the blood indirectly.

In some of the lower groups of animals the nutrient matter of the food, absorbed through the alimentary canal, merely passes from cell to cell throughout the body, or is received into a space or series of spaces containing fluid intervening between the alimentary canal and the wall of the body. But in the majority of animals there is a system of branching tubes containing a special fluid—the **blood,** and it is into this that the nutrient matter absorbed from the food sooner or later finds its way. The blood has for one of its principal functions the conveyance of the nutrient matters from the alimentary canal throughout the body, so that the various organs may select from it the material which they require for the carrying on of their functions.

The essence of the process of **respiration,** as we have already seen, is an interchange of oxygen and carbon dioxide which takes place between the tissues of an organism and the surrounding medium, whether air or water. The vital processes which go on in the animal-body, such as nervous and muscular activity, glandular secretion, and the production of heat and other forms of free energy, are more or less closely linked up with chemical processes of the

nature of oxidations. They therefore involve a constant consumption of oxygen, and usually lead to the formation of carbon dioxide. The necessary supply of oxygen has to be got from the air, or, in the case of aquatic animals, from the air dissolved in the surrounding water. At the same time the carbon dioxide has to be got rid of. In the lowest animals—as for instance Amœba, and many of higher organization—the oxygen passes inwards and the carbon dioxide outwards through the general surface of the body. But in the great majority of animals there is a special set of organs—the organs of respiration—having this particular function. In some animals these organs of respiration are processes, simple or branched, lined by a very delicate membrane, and richly supplied with blood-vessels. Such processes are called *gills* or *branchiæ*; they are specially adapted for the absorption of oxygen dissolved in water.

In other animals the oxygen is obtained from the air; and in such air-breathing forms the organ of respiration is very often a sac, either simple or compound, termed a *lung*. The interior of this sac is lined with an epithelium of extreme delicacy, immediately outside of which is a network of microscopic blood-vessels or *capillaries* with thin walls; and the oxygen readily passes from the air in the cavity of the lung through its lining and the thin wall of the blood-vessel into the blood, the carbon dioxide taking the opposite course. In other air-breathing forms the organs of respiration are *tracheæ*, ramifying tubes which open on the body-surface, their finest branches extending to all parts of the body. Through these tubes air is conveyed to and from the various organs, supplying the necessary oxygen and carrying away the carbon dioxide.

In order that the air or water in contact with the surface of the lungs or gills may be renewed, there are usually special mechanical arrangements. In many gill-bearing animals the gills are attached to the legs, and are thus moved about when the animal moves its limbs. In others certain of the limbs are constantly moving in such a way as to cause a current of water to flow over the gills. In air-breathing forms there is usually a pumping apparatus, by means of which the air is alternately drawn into and expelled from the lungs or the tracheæ.

In a great number of animals the blood contains a so-called *respiratory pigment*, usually a coloured protein compound containing a metal. These respiratory pigments enter freely into a loose chemical combination with oxygen, a process which is just as easily reversible. Thus the dark-red iron containing *hæmoglobin*, the best-known respiratory pigment, easily undergoes oxidation, being converted into bright-red oxyhæmoglobin. This splits up into hæmoglobin and oxygen whenever it comes into contact with tissues in which the oxygen tension is low. Such a substance is an ideal carrier for oxygen and greatly increases the efficiency of the blood-fluid in conveying the oxygen from the respiratory organs to the parts of the body where it is needed. Other

respiratory pigments containing iron are the red *hæmerythrin* and the green *chlorocruorin*. *Hæmocyanin*, which is present in many invertebrate animals, contains copper in its molecule, and on being oxidized changes from colourless to blue. The respiratory pigments are either dissolved in the blood-fluid or contained in so-called blood-corpuscles.

Another very important function of the blood is based upon the presence in it of colourless cells which actively move about and ingest solid particles, much in the same way as Amœba. These *amœboid* cells are to be found in the body-fluid and blood of lower and higher animals. By ingesting bacteria and other foreign bodies, which constantly find their way into the interior of the animal body, they form a powerful protective agent. Besides this, in higher animals, the blood has the power of forming chemical substances rendering the organism *immune* against certain germ-borne diseases. Finally, the blood acts as the carrier for a set of highly important chemical substances, the so-called *hormones*, which are secreted into the blood-stream by ductless glands. They serve in the co-ordination of processes going on in different parts of the body, and form an important means of communication between the various organs.

To carry out these functions the blood has to be made to circulate throughout the body. In the lowest forms in which a definite blood-system is to be recognized, this movement is effected in great measure by the general movements of the body of the animal. In others certain of the vessels contract and drive the blood through the system; such contractions are of a *peristaltic* character, the contractions being of the nature of constrictions running in a definite direction along the course of the vessel, with an effect similar to that produced by drawing the hand along a compressible india-rubber tube.

In all higher forms the movement of the blood is effected by means of a special organ—the *heart*. The heart is a muscular organ which by its contractions forces the blood through the system of vessels. In its simplest form it usually consists of two chambers, both with muscular walls—the one, called the *auricle*, receiving the blood and driving it into the other, which is called the *ventricle*. The latter, in turn, when it contracts, drives the blood through the vessels to the various parts of the body—the return of the blood backwards to the auricle from the ventricle being prevented by the presence of certain *valves*, which act like folding doors opening from the auricle towards the ventricle, but closing when pressure is exerted in the opposite direction. In the higher animals the heart becomes a more complex organ than this, with a larger number of chambers and a more elaborate system of valves.

Carbon dioxide, as already mentioned, is a waste-product constantly being produced in the tissues and being carried off by the blood to pass out by the gills or lungs. Besides the carbon dioxide there are constantly being formed waste-substances of another class—viz., substances containing nitrogen, of which *ammonia*, *urea*, and *uric acid* are the principal ultimate forms. These

are separated from the blood and thrown out of the body by a distinct set of organs called **renal organs,** or **organs of urinary excretion.** The form of these organs varies greatly in the different groups; in many cases they are more or less intimately connected with the genital system.

The essential elements of the **reproductive organs**—the *ova* and *spermatozoa*—have already been briefly described (p. 20). The ova are developed in an organ termed the *ovary*, and the sperms in an organ called the *testis.* Sometimes ovaries and testes are developed in the same individual, which is then called *monœcious* or *hermaphrodite*; sometimes the ovaries occur in one set of individuals—the females—and the testes in another set—the males—when the term *unisexual* or *diœcious* is employed. Very frequently the male differs from the female in other respects besides the nature of the reproductive elements—in size, colour, and the like; when such differences are strongly marked the animal is said to be *sexually dimorphic.* The ova and sperms are usually conveyed to the exterior by canals or ducts—the ovarian ducts or *oviducts*, and the testicular ducts or *vasa deferentia.* In some instances the ova are fertilized after being discharged from the oviducts, and the development of the young takes place externally; in other cases the fertilization takes place in the oviduct, and the young become fully developed in the interior of a special enlargement of the oviduct termed the *uterus.* In the former case the animal is said to be *oviparous*, in the latter *viviparous*; but there are numerous intermediate gradations between these two extremes.

6. The Reproduction of Animals.

In a limited number of groups of animals reproduction takes place by means of cells corresponding to ova developed in organs similar to ovaries, but without fertilization by means of sperms. This phenomenon is known as **parthenogenesis.**

Besides the sexual process of reproduction by means of ova and spermatozoa, there are in many classes of animals various **asexual** modes of multiplication. One of these—the process of *simple binary fission*—has been already noticed in connection with the reproduction of Amœba. The formation of "*spores*" by *multiple fission* is an asexual mode of multiplication which occurs only in the Protozoa, and will be described in the account of that group. Multiplication by *budding* takes place in a number of different classes of animals. In this form of reproduction a process or *bud* (Fig. 32) is given off from some part of the parent animal; this bud sooner or later assumes the form of the complete animal, and may become detached from the parent either before or after its development has been completed, or may remain in permanent vital connection with the parent form.

When the buds, after becoming fully developed, remain in vital continuity with the parent, a sort of compound animal, consisting of a greater or smaller

number of connected units, is the result. Such a compound organism is termed a *colony*, and the component units are termed *zooids*. In some cases such a colony is produced by a process which is more correctly termed *incomplete fission* than budding.

Alternation of Generations; Heterogamy; Pædogenesis.—In the life-history of a considerable number of animals, a stage in which reproduction takes place by a process of budding or fission alternates with a stage in which there occurs a true sexual mode of reproduction. Such a phenomenon is termed *alternation of generations* or *metagenesis*. The term *heterogamy* is applied to cases in which two different sexual generations—usually a true sexual and a parthenogenetic—alternate with one another. *Pædogenesis*, or the development of young from individuals that have not attained the adult condition, is a phenomenon which is to be observed in some groups of animals.

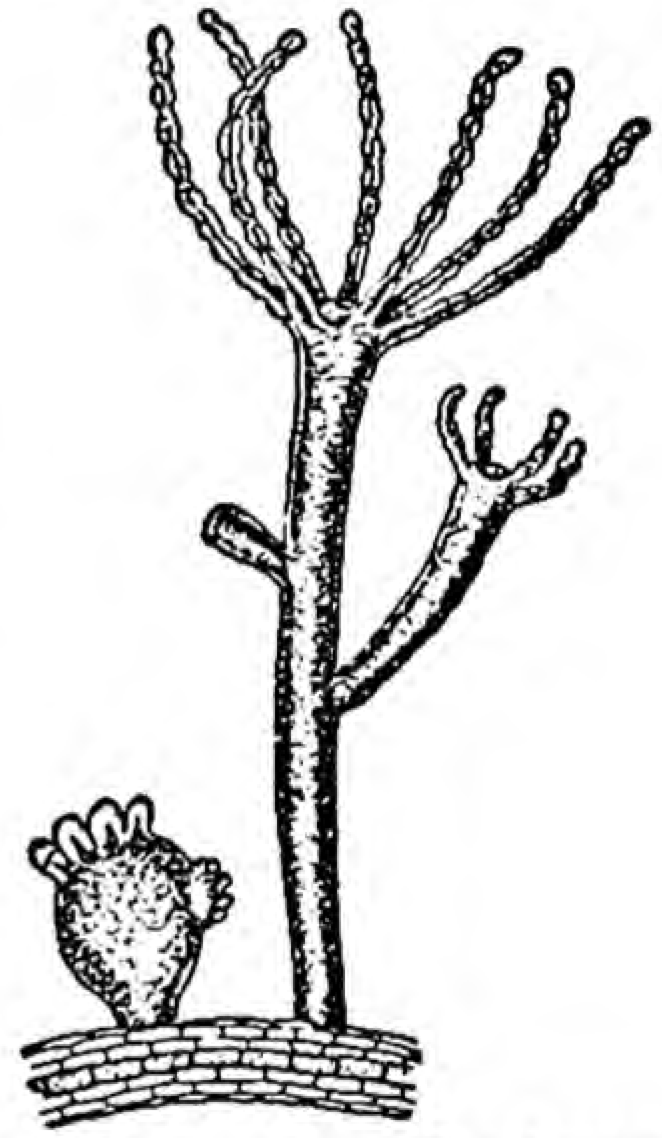


FIG. 32.—Freshwater polype (**Hydra**); two specimens, the one expanded, the other contracted, showing multiplication by budding. (From Newman, after Pfurtscheller and Parker.)

7. Symmetry.

The general disposition or **symmetry** of the parts in an animal presents two main modifications—the *radial* and the *bilateral*. The *gastrula* (p. 24) is the simplest and most generalized form among multicellular animals or Metazoa; but no adult animal retains this simple shape. In the gastrula we may imagine a central *primary axis* (Fig. 33, *A B*) passing through the middle of the blastopore and of the archenteric cavity, and a series of *secondary axes* (*ab*, *cd*) running at right angles to this to the outer surface. In a symmetrical gastrula the secondary axes would be all equal. Many animals are in the adult condition similar in their symmetry to the gastrula, except that there are special developments along a series of regularly arranged radiating secondary axes; these radial developments may be in the form of tentacles or radially arranged processes (Fig. 34), or may assume the character of a radial arrangement of internal parts. Such an animal is said to be *radially symmetrical*. The body of a radially symmetrical animal is capable of being divided into a series of equal radial parts or *antimeres*, each of which is symmetrically disposed with regard to one of the secondary or radial axes.

In animals which are not permanently fixed, locomotion usually takes place in the direction of the primary axis of the body, and one side, habitually directed downwards, becomes modified differently from the other, which is habitually directed upwards: a *lower* or *ventral* surface becomes distinguishable from an *upper* or *dorsal*. Thus the radial symmetry is now disturbed; the

secondary axes have become unequal; the *dorso-ventral* or *vertical* secondary axes are, to a greater or less extent, different from the *transverse* or *horizontal* secondary axes, and the body of an animal having such a disposition of the parts is divisible into two equal lateral halves by a median vertical plane passing through the primary axis. This is the *bilateral symmetry* observable in all but a few types of animals.

Sometimes the bilaterally symmetrical animal is unsegmented; sometimes

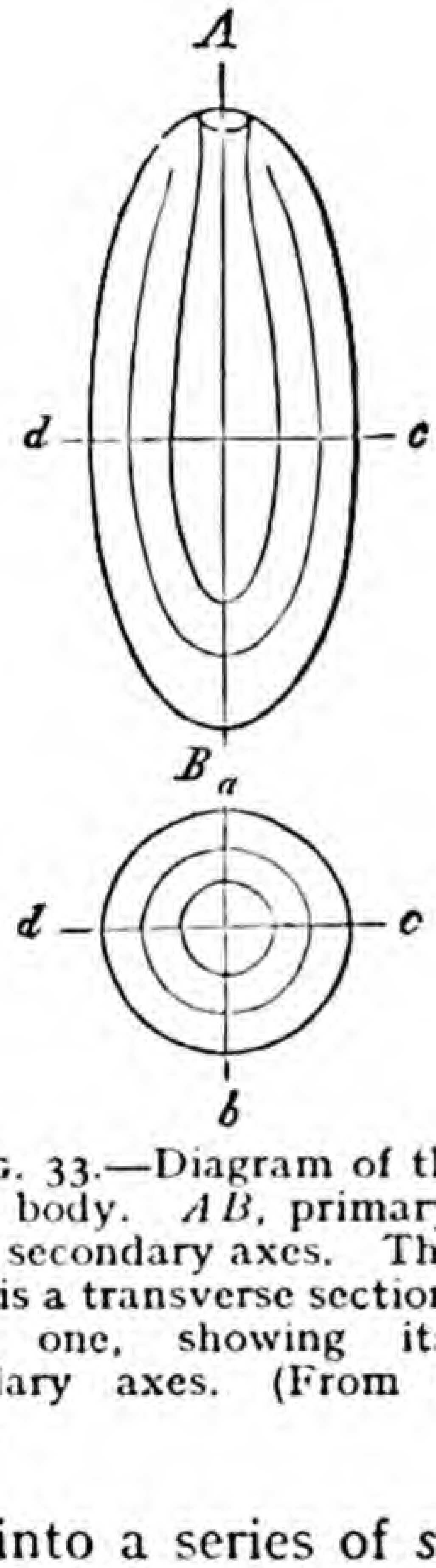


FIG. 33.—Diagram of the axes of the body. *AB*, primary axis; *ab*, *cd*, secondary axes. The lower figure is a transverse section of the upper one, showing its two secondary axes. (From Gegenbaur.)

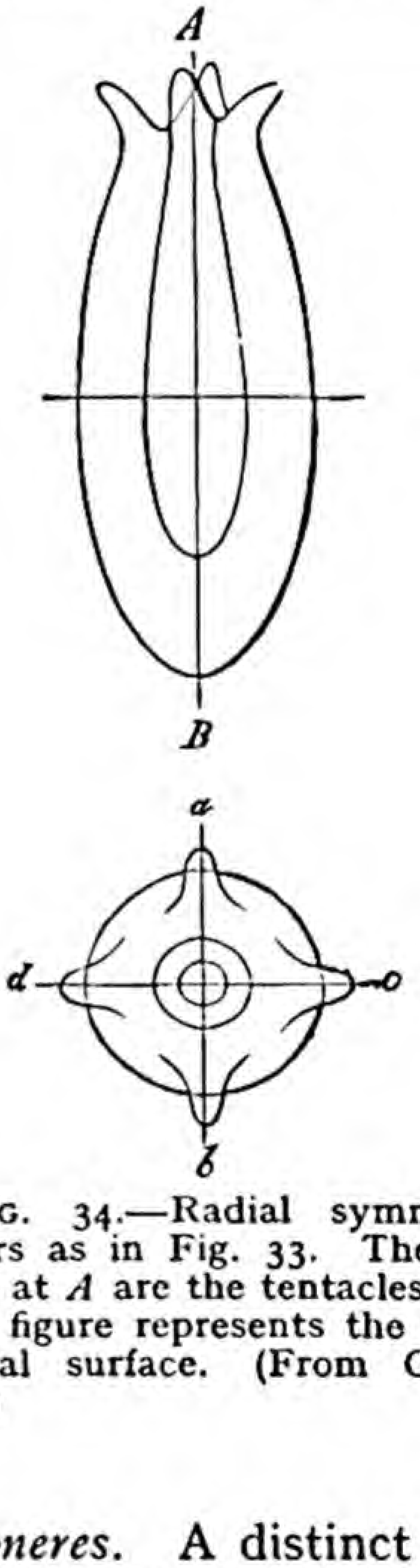


FIG. 34.—Radial symmetry. Letters as in Fig. 33. The processes at *A* are the tentacles; the lower figure represents the upper or oral surface. (From Gegenbaur.)

it is divided into a series of *segments* or *metameres*. A distinct *head* may be present or absent. The head end or anterior end is that which, save in exceptional cases, is directed forwards in locomotion. It is towards this end that the sense-organs are situated, as well as the opening of the mouth and the organs for the prehension and mastication of food. A head is developed when the anterior part bearing these structures is marked off externally from the rest. In segmented animals the head consists of a number of segments amalgamated together, and it contains the brain or the principal central ganglia of the nervous system.

SECTION II

SUB-KINGDOM AND PHYLUM PROTOZOA

THE Protozoa of which Amœba is an example are *non-cellular* organisms—*i.e.*, the body of the individual animal is not subdivided into cells, as is the case in the so-called *cellular* animals the Parazoa and Metazoa. Very frequently the Protozoa are described as *unicellular* animals as opposed to the *multicellular* Parazoa and Metazoa. This is based on the assumption that the body of a free living protozoon is homologous to a single metazoan body-cell. This speculative assumption tends to minimize the intrinsic difference between the protozoan organism as a free living whole and the cell as the more or less specialized smallest unit of which the organs of the metazoan body are built up. There is, however, at least a formal similarity between the different types of metazoan cells and the external shape of various protozoa. We have learnt that cells may be *amœboid*, or capable of protruding temporary processes of protoplasm called pseudopods; *flagellate*, or produced into one or more—always a small number—of threads having an intermittent lashing movement; *ciliated*, or produced into numerous rhythmically moving threads of protoplasm. Moreover, under certain circumstances, amœboid cells may fuse with one another to form a *syncytium* or *plasmodium*.

These well-marked differences in shape are the guiding principle in the subdivision of the Protozoa into *Classes*. The same organism may be amœboid, flagellate, encysted (the protoplasm being enclosed in a cell-wall), and plasmodial at various stages of its existence, but nevertheless we find certain forms in which the dominant phase in the life-history is amœboid, others which are characteristically flagellate or ciliated, others again in which the tendency to form plasmodia is a distinctive feature. In this way five well-marked groups of unicellular organisms may be distinguished.

Class 1. RHIZOPODA.—Protozoa in which the amœboid form is predominant, the animal always forming pseudopods. Flagella are often present during some period of their life-history. Encystation frequently occurs.

Class 2. MYCETOZOA.—Terrestrial Protozoa in which the plasmodial phase is specially characteristic, as also is the formation of large and often complex cysts.

Class 3. MASTIGOPHORA (FLAGELLATA).—Protozoa in which the flagellate form is predominant, although the amœboid and encysted conditions frequently occur.

Class 4. SPOROZOA.—Parasitic Protozoa without special locomotory parts in

the adult. Encystation is almost universal, and there may be flagellate or amœboid stages in the life-history.

Class 5. CILIOPHORA.—Protozoa which are always ciliated, either throughout life or in the young condition.

CLASS I.—RHIZOPODA.

I. EXAMPLE OF THE CLASS—*Amœba proteus.*

Amœba has been fully described in the preceding section; it will therefore

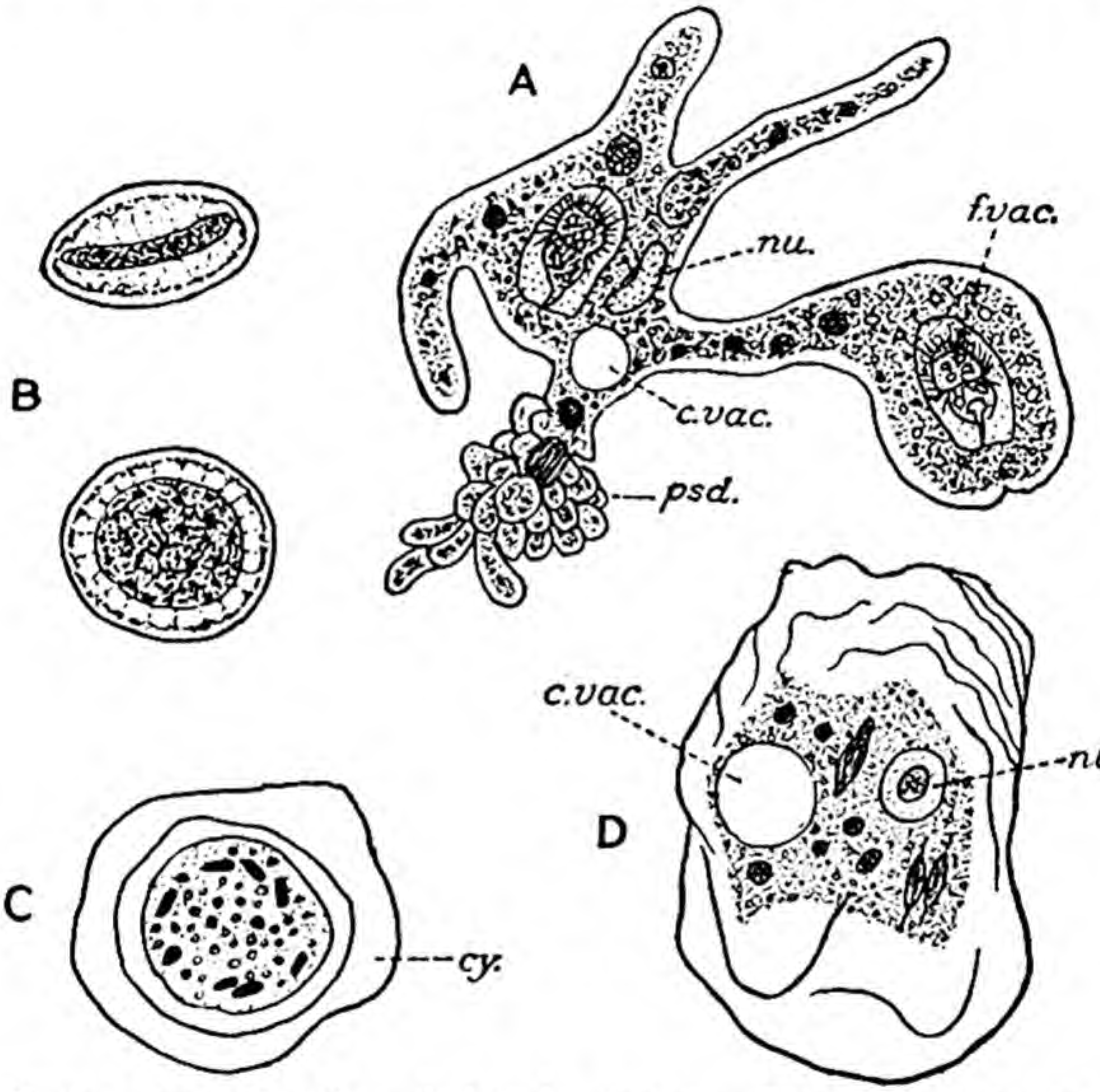


FIG. 35.—Two species of **Amœba.** *A*, Amœba proteus; *B*, nucleus of *A. proteus*, lateral and top views; *C*, *A. proteus*, encysted; *D*, *Amœba verrucosa*; *c. vac.* contractile vacuole; *cy.* cyst; *f. vac.* food vacuole; *nu.* nucleus; *psd.* pseudopods. (From Parker's Biology and Doflein-Reichenow's *Lehrbuch der Protozoenkunde* (Gustav Fischer, Jena).)

be unnecessary to do more than recapitulate the most essential features in its organization.

Amœba is an irregular mass of protoplasm (Fig. 35, *A*) about $\frac{1}{8}$ mm. in diameter, produced into irregular processes or *pseudopods* (*psd.*) of variable size and form and capable of being protruded and retracted, often with considerable rapidity. The protoplasm is divisible into a granular internal substance, the *endosarc* or *endoplasm*, and a clear outer layer, the *ectosarc* or *ectoplasm*; the difference between the two is hardly a structural one, but

depends simply on the accumulation of granules in the central portion. The granules are, for the most part, various products of metabolism.

Imbedded in the endosarc is a large *nucleus* (*nu.*), of spherical form, consisting of a clear achromatic substance, enclosed in a membrane, and containing minute granules of chromatin. The *contractile vacuole* (*c. vac.*), a very characteristic structure of the Protozoa, lies in the outer layer of the endosarc, and exhibits rhythmical pulsations, taking up fluid from the protoplasm around it and discharging it to the outside at more or less regular intervals. The function of this structure, as far as it occurs in fresh-water protozoa, is the establishment of an *osmotic balance* between the interior of the animal and its surroundings. Owing to a higher osmotic pressure in the interior, water is continually taken up from outside and has to be removed. If the activity of the contractile vacuole is experimentally inhibited, the protozoon swells and may finally burst.

Amœba feeds by ingesting minute organisms (Fig. 35, *A*, *f. vac.*) or fragments of organisms—*i.e.*, by enveloping them in its substance, retaining them until the digestible matter they contain is dissolved and assimilated, and then crawling away and leaving the undigested remnants behind.

Amœbæ are sometimes found to undergo *encystation*; the pseudopods are withdrawn and the protoplasm surrounds itself with a cell-wall or *cyst* (*D*, *cy.*), from which, after a period of rest, it emerges and resumes active life.

Reproduction takes place in *Amœba proteus* by *binary fission*; division of the nucleus is followed by division into two of the cell-body. Occasionally two Amœbæ have been observed to *copulate* or undergo complete fusion, but nothing is known of the result of this process or of its precise significance in this particular case.

2. Classification and General Organization.

The Rhizopoda differ among themselves in the character of their pseudopods, which may be short and blunt or long and delicate; in the number of nuclei; and in the presence or absence of a hard shell within or around the protoplasm. The following five orders may be distinguished :—

Order 1.—Lobosa.

Rhizopoda with short, blunt pseudopods. There is a clear distinction between ectoplasm and endoplasm.

Examples: *Amœba* (Fig. 35), *Quadrula* (Fig. 36).

Order 2.—Filosa.

Rhizopoda with fine branched pseudopods which do not fuse except near the bases: no ectoplasm.

Example: *Euglypha* (Fig. 38).

ORDER 3.—FORAMINIFERA.

Shelled Rhizopoda with fine, branched, and anastomosing pseudopods. Example: *Polystomella* (Fig. 44).

ORDER 4.—HELIOZOA.

Rhizopoda with fine, stiff, radiating pseudopods. Example: *Actinosphærium* (Fig. 46).

ORDER 5.—RADIOLARIA.

Rhizopoda having a shell in the form of a perforated central capsule, and usually, in addition, a siliceous skeleton: the pseudopods are long and delicate. Examples: *Lithocircus* (Fig. 39), *Actinomma* (Fig. 51), *Collozoum* (Fig. 52).

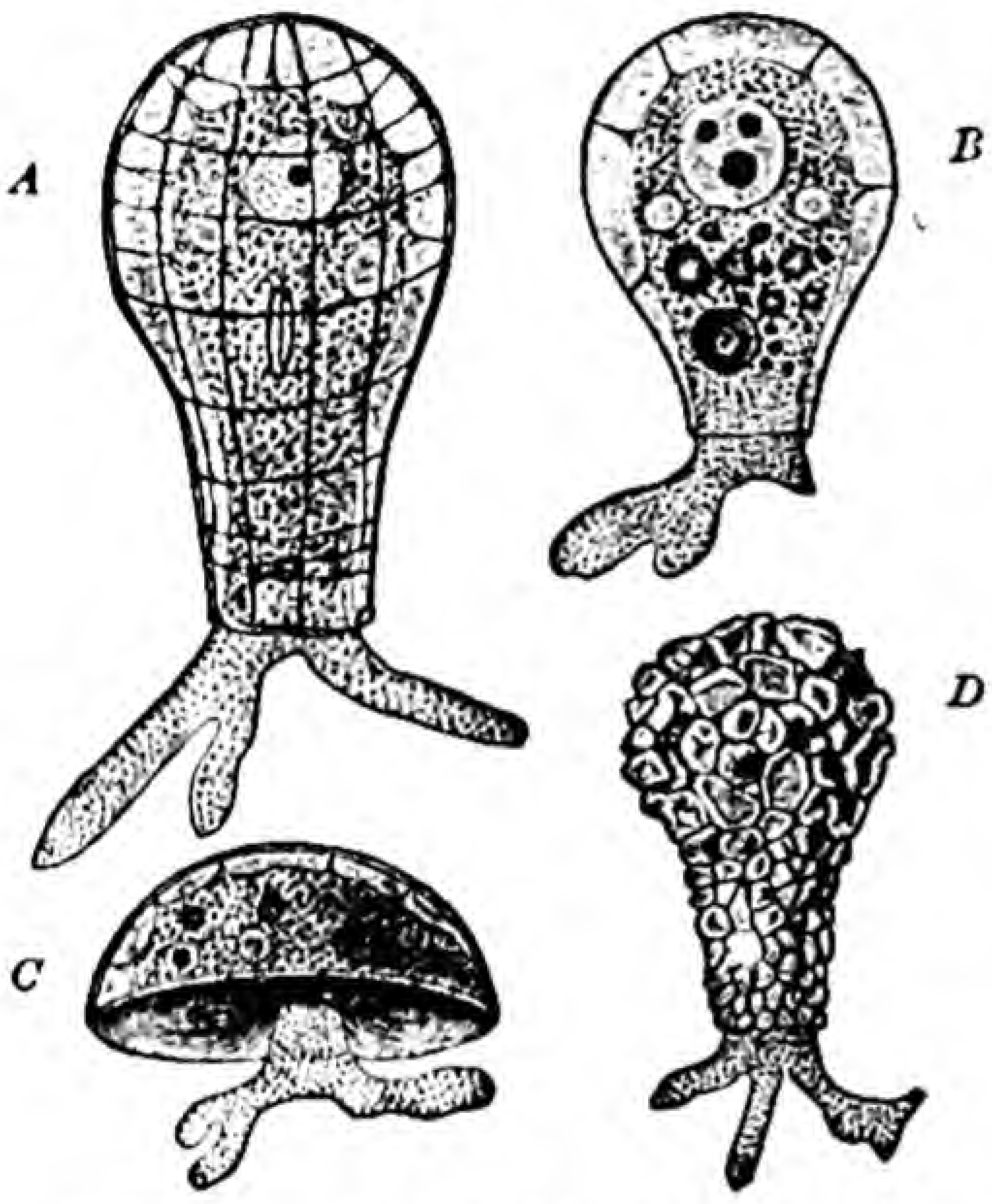


FIG. 36.—*A*. **Quadrula symmetrica**; *B*. **Hyalosphenialata**; *C*. **Arcella vulgaris**; *D*. **Difflugia pyriformis.** (From Lang's *Comparative Anatomy*.)

ORDER 1.—LOBOSA.

General Structure.—The members of this group all agree with Amœba in essential respects, their most characteristic feature being the short, blunt pseudopods. The chief variations in structure upon which the genera and species are founded have to do with the number and character of the nuclei, the form of the pseudopods, and the presence or absence of a shell.

In Amœba itself there may be one or several nuclei, the chromatin of the nucleus may be arranged in various ways, and the pseudopods may be prolongations of considerable relative size (Fig. 35, *A*), or mere wave-like elevations of the surface (Fig. 35, *D*).

The largest of the naked or shell-less Lobosa is *Pelomyxa*, which may be as much as 8 mm. in diameter; it is multi-nucleate and is further distinguished by the apparent absence of contractile vacuoles.

Skeleton.—We may understand the relation of the shelled to the shell-less Lobosa by supposing an Amœba to draw in the pseudopods from the greater part of its body, and to secrete, from that part only, a cell-wall; such a cell-wall or capsule would differ from a cyst in having an aperture at one end to allow of the protrusion of pseudopods from a small naked area. This is exactly what we find in *Arcella* and its allies (Fig. 36, *A–C*), in which the shell is chitinoid. A different kind of shell is found in *Difflugia* (*D*), which secretes a gelatinous coating to which minute sand-grains and other foreign particles become attached.

The prevailing mode of **multiplication** is by means of binary fission. But multiple fission also occurs. In such a case the animal frequently passes into the encysted condition, and nucleus and protoplasm undergo a process of division resulting in the formation of a number of small bodies or *merozoites* which, when mature, are set free by the rupture of the wall of the cyst. Each of these may develop directly into the adult form. But in some cases it has been found that

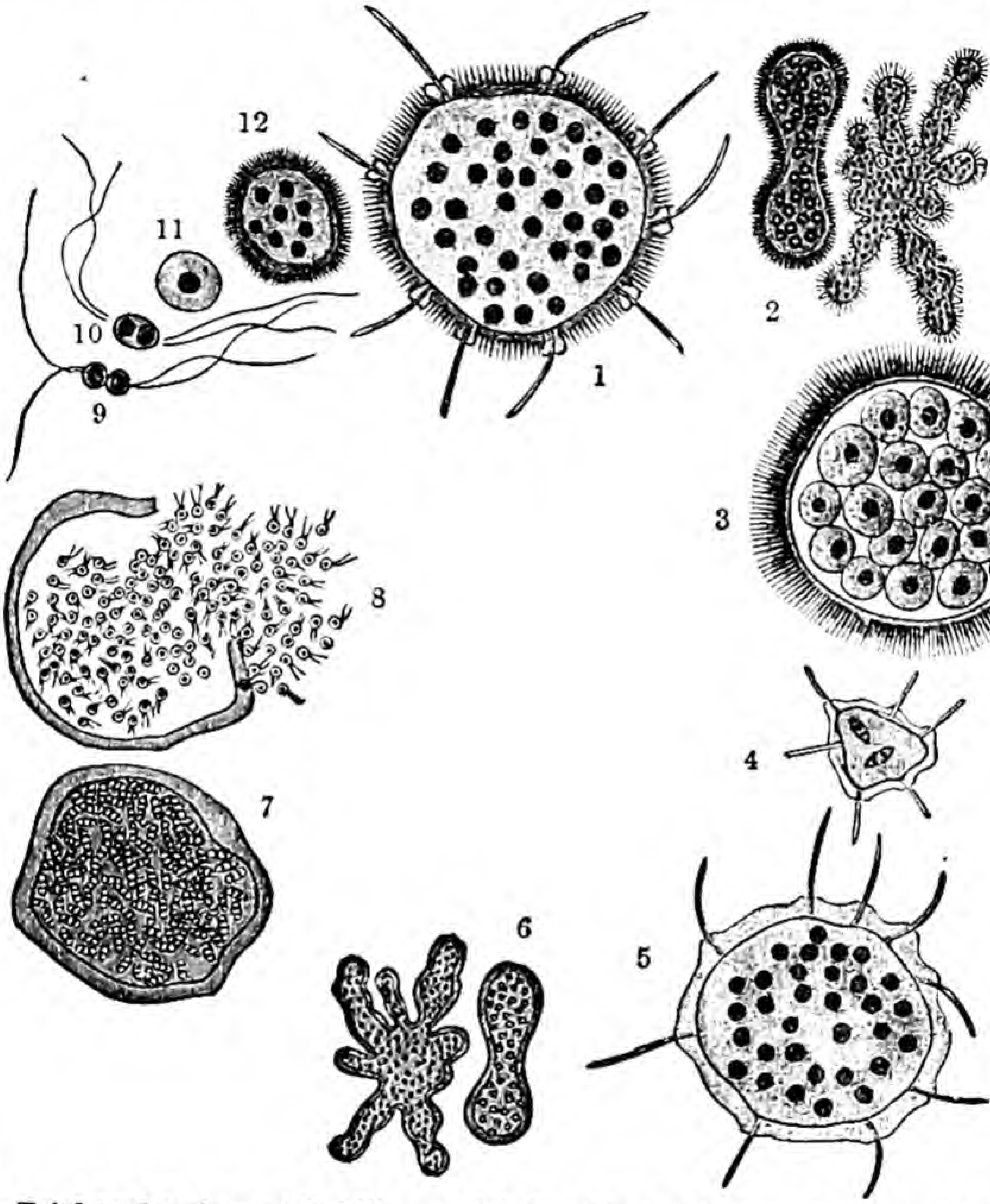


FIG. 37.—**Trichosphærium sieboldii.** *1*, Adult of "A" form; *2*, its multiplication by fission and gemmation; *3*, division into amœboid spores; *4*, development of one of these into "B" form (*5*); *6*, its multiplication by fission and gemmation; *7*, its division into numerous minute bodies; *8*, discharge of these as biflagellate gametes; *9*, *10*, copulation, more highly magnified; *11*, zygote; *12*, transition towards "A" form. (After Schaudinn.)

on becoming free from the cyst they coalesce in pairs either with one another or with similar bodies from other cysts. To such a coalescence, which extends to the two nuclei as well as the cytoplasm, the term *copulation* or *syngamy* is applied—the two copulating bodies being *gametes* and the body resulting from the union a *zygote*. This is the simplest form of sexual reproduction. In *Trichosphærium* (Fig. 37) there is an alternation of generations—one generation (*1*, *2*) reproducing by fission and gemmation (budding) and then breaking up into

amœboid merozoites (*3*) which do not copulate but develop (*4*) directly into the second generation (*5*), and this after reproducing by fission and gemmation (*6*), becomes resolved into bi-flagellate gametes (*7*, *8*), which copulate in pairs with other similar gametes (*9*, *10*, *11*), the zygotes developing into the first generation (*12*). In some cases copulation takes place, not between specially produced gametes, but between adults (*hologamy*); this is usually followed either by more active multiplication or by passing into a motionless resting condition.

Most of the Lobosa are free; some occurring in fresh water, others in the soil, others in the sea. But a number are parasites in the bodies of higher animals. A number of species of Amœba are known to occur as parasites in man, of which *Entamœba histolytica* has been proved to be pathogenic, causing dysentery and liver abscess.

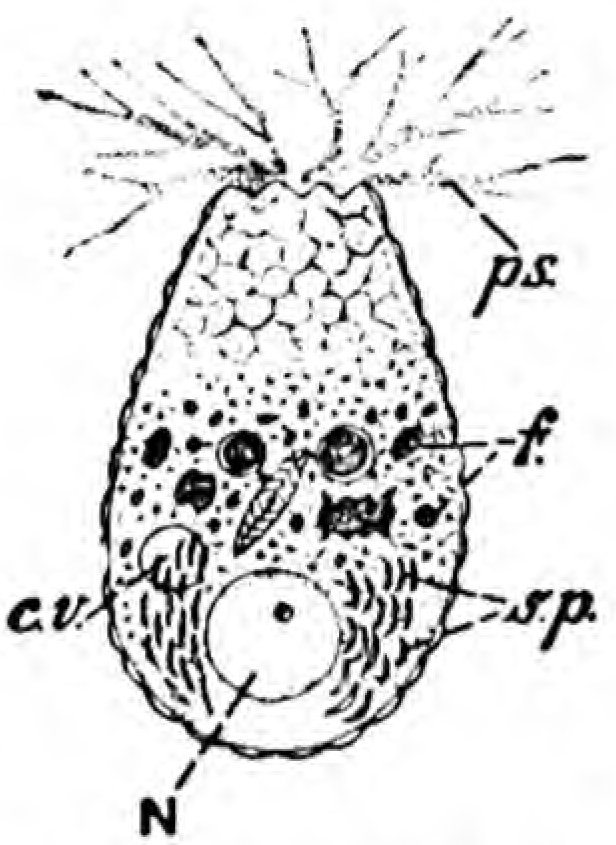


Fig. 38.—**Euglypha alveolata.** *c. v.* contractile vacuole; *f.* food material; *N.* nucleus; *ps.* pseudopodia; *s. p.* reserve shell plates. (From Minchin's *Introduction to the Study of the Protozoa* (Edward Arnold), after Schewiakoff.)

Order 2.—Filosa.

The order Filosa comprises a small number of Rhizopods having affinities with some of the Lobosa on the one hand and with the Foraminifera on the other. The pseudopodia are very fine and thread-like, and become branched towards the ends: unlike those of the Foraminifera, they do not coalesce with one another except at or near the proximal ends, and do not form networks. There is no clear ectoplasmic layer. The best known of the Filosa—*Euglypha* (Fig. 38)—has a flask-shaped test composed of close-fitting hexagonal siliceous plates.

Order 3.—Foraminifera.

General Structure.—The members of this order differ from the Lobosa in the fact that their pseudopods are long and delicate and unite to form networks; moreover, with few exceptions, they agree with Arcella and its allies in possessing a shell. In the majority of cases this shell is formed of calcium carbonate.

One of the simplest members of the group is *Microgromia* (Fig. 39). It consists of a protoplasmic body (*B*), with a single nucleus (*nu.*) and contractile vacuole (*c. vac.*), enclosed in a chitinoid cell-wall or shell (*sh.*) with an aperture at one end through which the protoplasm protrudes and is produced into delicate radiating pseudopods. The animal multiplies by binary fission, and the individuals or *zooids* thus produced remain united in larger or smaller clusters, or cell-colonies (*A*). Sometimes the cell-body of a zooid divides and one of the daughter-cells creeps out of the cell-wall (*C*), and, after moving about for a time like an Amœba, draws in its pseudopods, assumes an oval form, and sends

out two flagella, by means of which it is propelled through the water (*D*). We shall find other instances in which the young of a Rhizopod is a *flagellula*—*i.e.*, a cell provided with one or more flagella, which, if its history were not known, would be included among the Mastigophora.

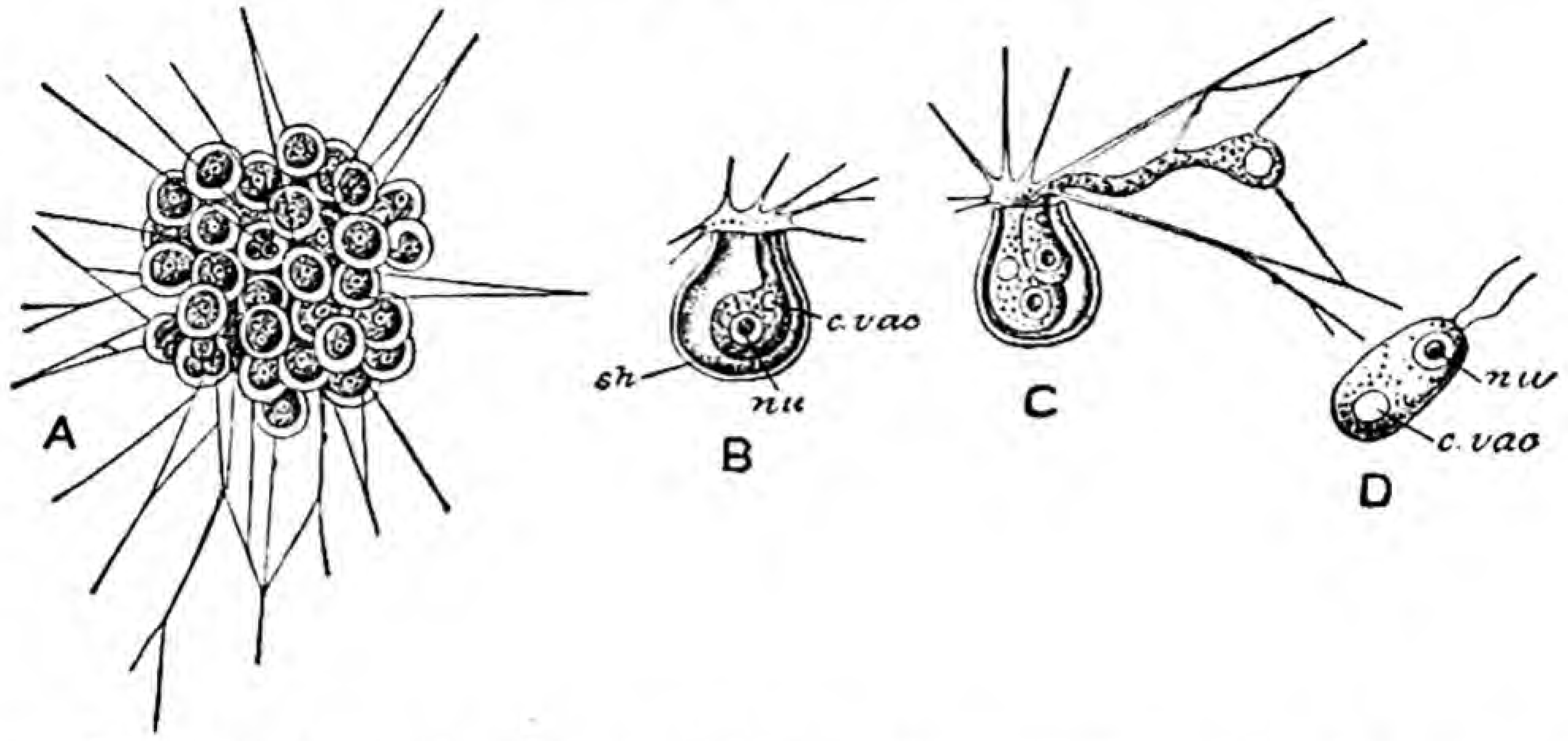


FIG. 39.—**Microgromia socialis.** *A*, entire colony; *B*, single zooid; *C*, zooid which has undergone binary fission, with one of the daughter-cells creeping out of the shell; *D*, flagellula; *c. vac.* contractile vacuole; *nu.* nucleus; *sh.* shell. (From Bütschli's *Protozoa*, after Hertwig and Lesser.)

Chlamydophrys stercorea (Fig. 40) is a form resembling Microgromia. In the simple condition it has a chitinous shell with a single narrow opening;

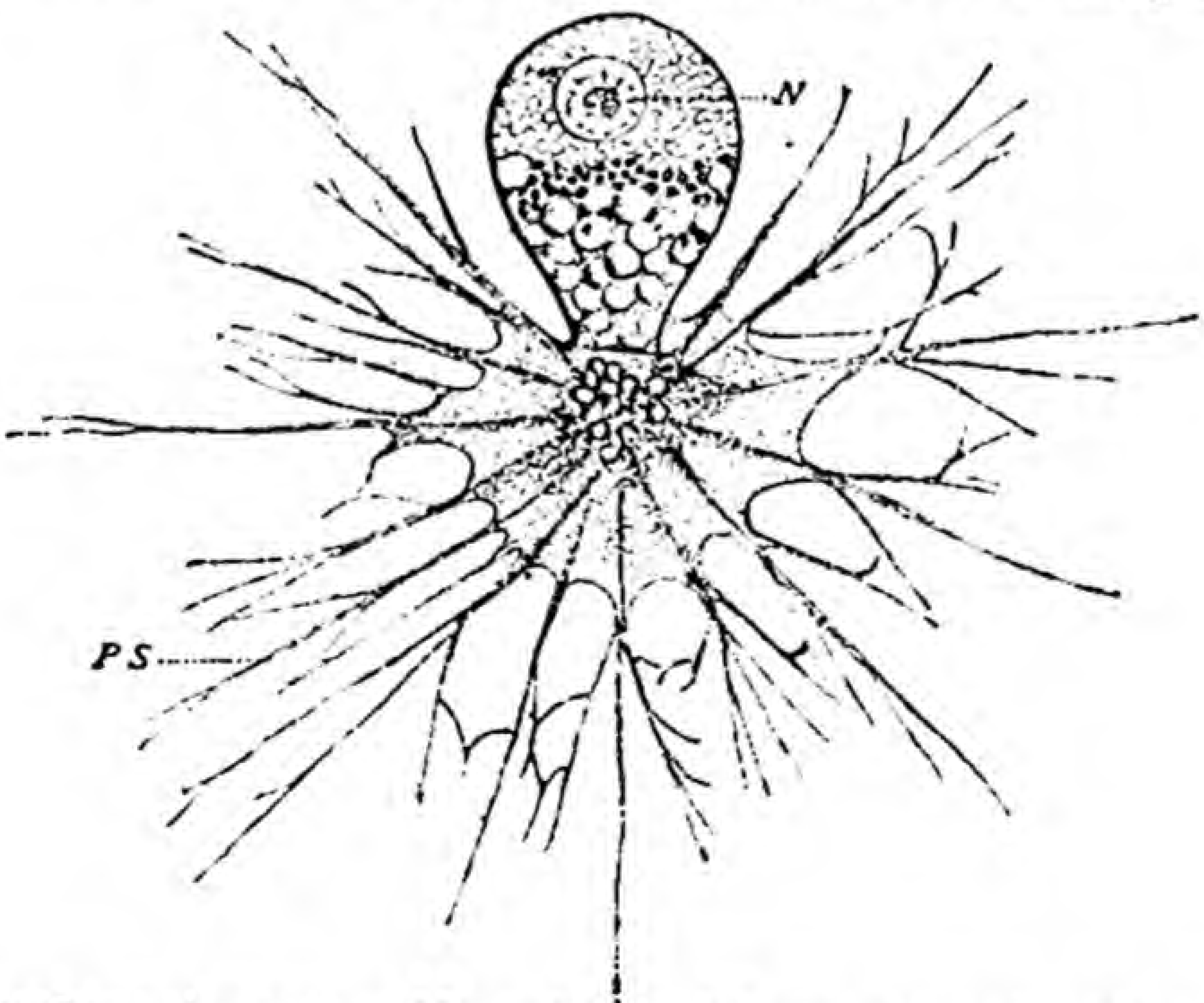


FIG. 40.—**Chlamydophrys stercorea.** *N.* nucleus; *PS.* pseudopod. (From Doflein-Reichenow's *Lehrbuch der Protozoenkunde* (Gustav Fischer, Jena).)

it multiplies by binary fission, and by multiple fission produces gametes which copulate. The resulting zygote forms a cyst which has to pass through the intestine of Man or another mammal in order to develop into an amœboid phase which, surrounding itself with a shell, develops into a typical Chlamydophrys. As a parasite it is said to be harmless.

Allogromia (Fig. 41, *1*) leads us to the more typical Foraminifera. The protoplasm of this form protrudes from the mouth (*a.*) of the chitinoid shell (*sh.*), and flows around it so that the shell becomes an internal structure. The pseudopods are very long and delicate, and unite to form a complicated net-

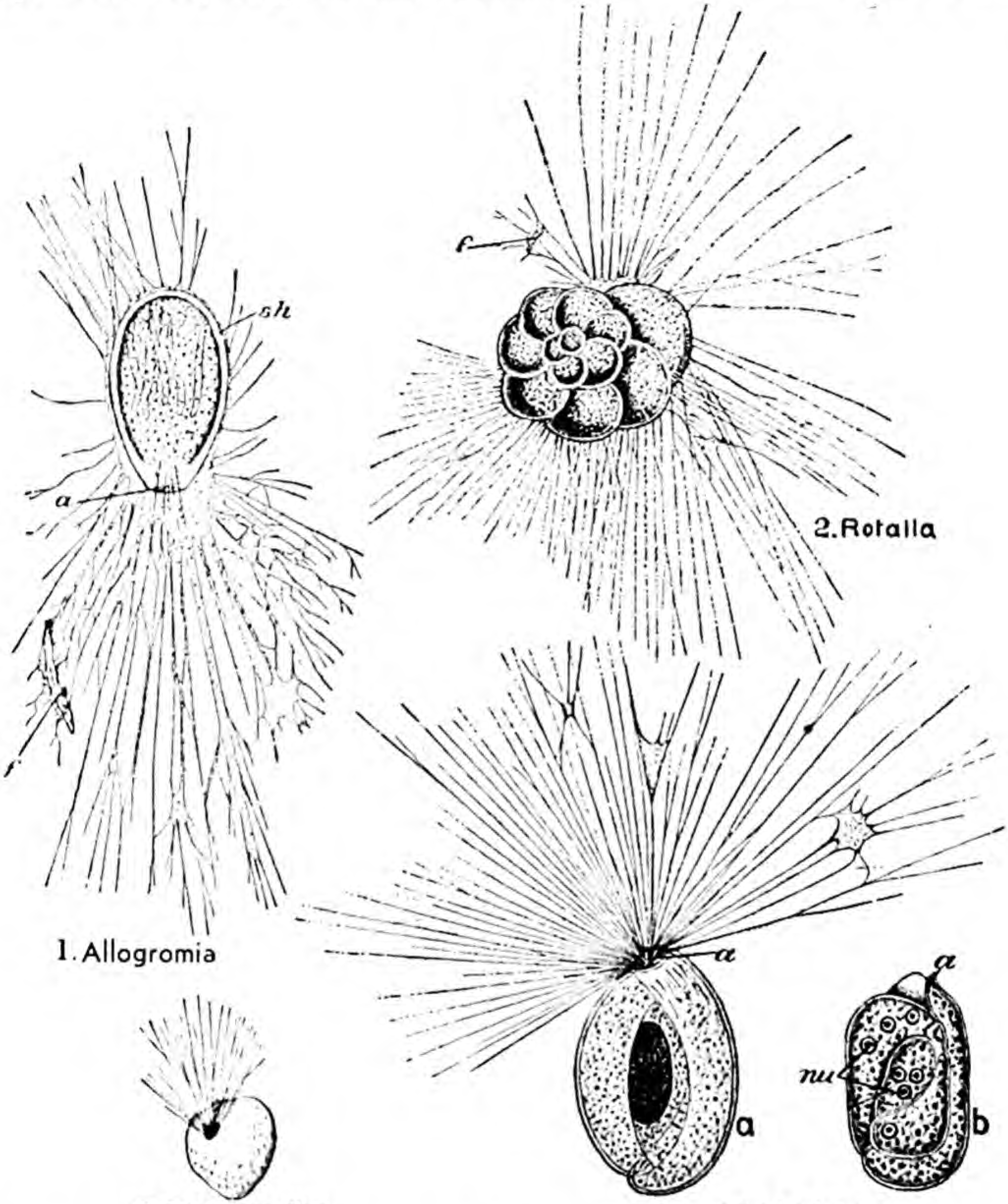


FIG. 41.—Various forms of **Foraminifera.** In *4*, Miliola, *a*, shows the living animal; *b*, the same killed and stained; *a*. aperture of shell; *f*. food particles; *nu*. nucleus; *sh*. shell. (From Bütschli's *Protozoa* and *Claus's Zoology*.)

work, exhibiting a streaming movement of granules and serving, as usual, to capture prey.

Skeleton.—*Squammulina* (Fig. 41, *3*) differs from Allogromia mainly in having the shell formed of calcium carbonate and possessing the character of a

hollow, stony sphere, with an aperture at one end. It appears that all the calcareous Foraminifera begin life in this simple form; but in the majority of cases the adult structure attains a considerable degree of complexity. The protoplasm of the original globular chamber overflows, as it were, through the

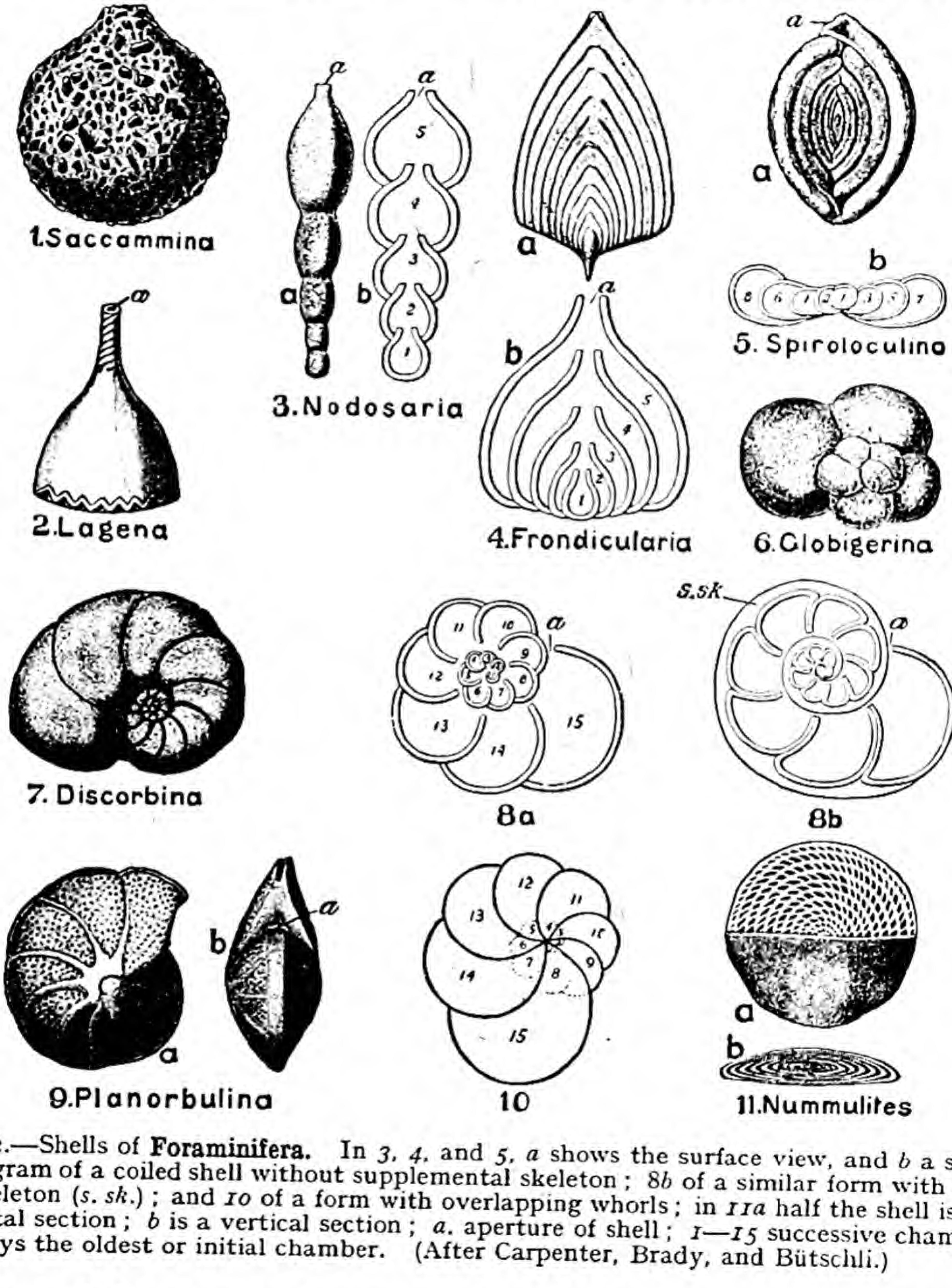


FIG. 42.—Shells of **Foraminifera.** In *3, 4,* and *5, a* shows the surface view, and *b* a section; *8a* is a diagram of a coiled shell without supplemental skeleton; *8b* of a similar form with supplemental skeleton (*s. sk.*); and *10* of a form with overlapping whorls; in *11a* half the shell is shown in horizontal section; *b* is a vertical section; *a.* aperture of shell; *1—15* successive chambers, *1* being always the oldest or initial chamber. (After Carpenter, Brady, and Bütschli.)

aperture; and the extruded mass rounds itself off, and secretes a calcareous shell in organic connection with the original shell, and communicating with it by the original aperture. In this way a two-chambered shell is produced, and a repetition of the process gives us the many-chambered shell found in most genera. New chambers may be added in a straight line (Fig. 42, *3*), or alter-

nately on opposite sides of the original chamber (*5*), or with each new chamber enclosing its predecessor (*4*), or in a flat spiral, each new chamber being larger than its predecessor (*7, 8*), or in a spire in which the newer chambers overlap the older (*9, 10*), or in an irregular spiral of globular chambers (*6*), or in an extremely compact spiral in which the new chambers completely enclose their predecessors (*11*). In all cases adjacent chambers communicate with one another either by a single large hole or by numerous small ones: the protoplasm is thus perfectly continuous throughout the organism. With the increase in the number of chambers there is a multiplication of the nucleus (Fig. 41, *4b, nu.*).

The shell presents two leading types of structure apart from the form and arrangement of the chambers: either it is of a dense porcelain-like texture and

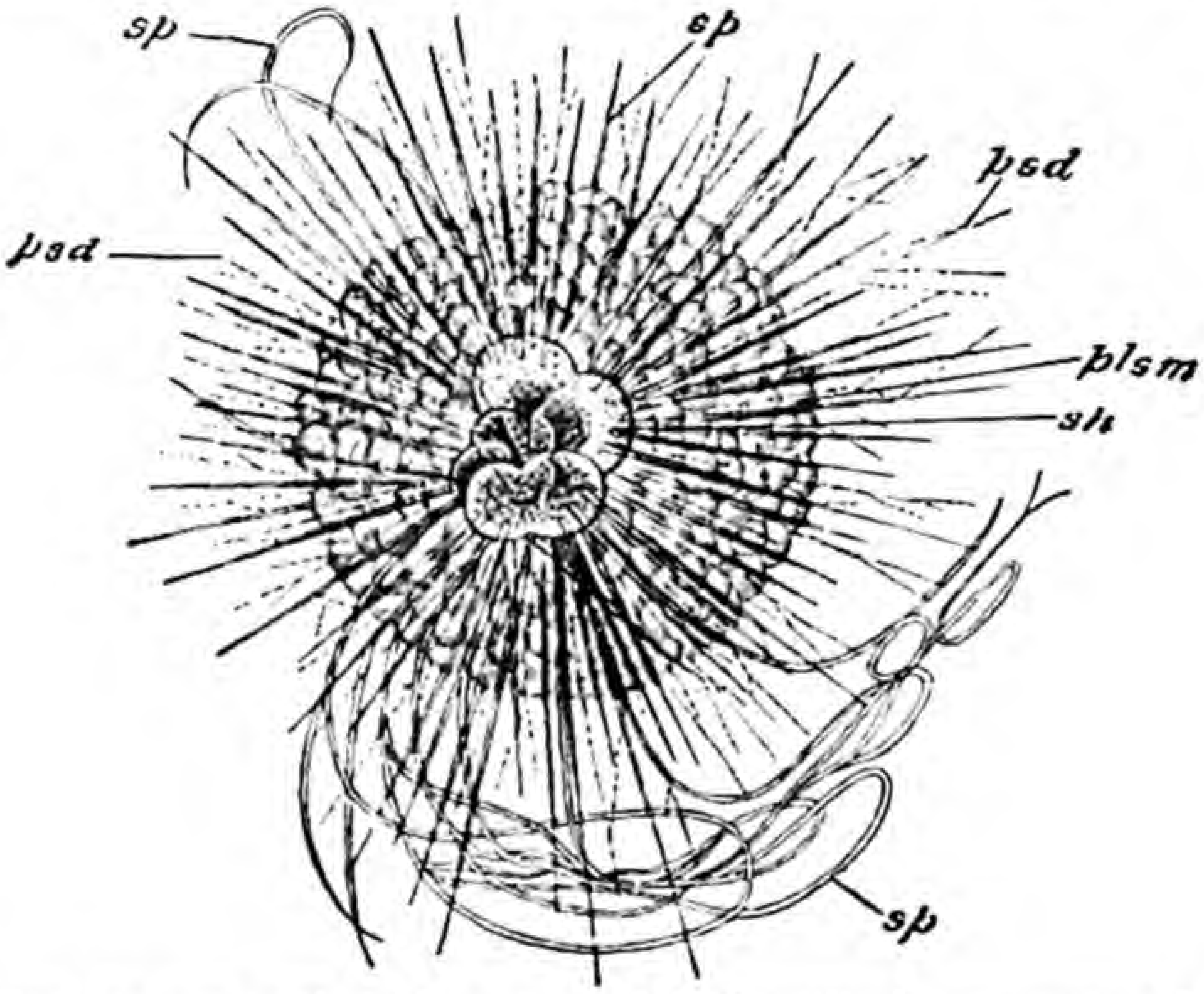


FIG. 43.—**Hastigerina murrayi.** *plsm.* vacuolated protoplasm surrounding shell; *psd.* pseudopods; *sh.* shell; *sp.* spines. (After Brady.)

provided with a single terminal aperture (*imperforate*, Fig. 41, 4), or the texture is more open and the whole shell is perforated with very minute apertures, through which, as well as through the terminal aperture, pseudopods are protruded (*perforate*, Fig. 41, *2*).

In many cases additional complexity is attained by the development of an elaborate canal system in the more complicated perforate forms, and, in certain cases, of what is called the *supplemental skeleton* (Fig. 42, *8b, s. sk.*). This consists of a deposit of calcium carbonate outside the original shell; it is traversed by a complex system of canals containing protoplasm and is sometimes produced into large spines. Foraminifera in which this secondary skeleton occurs are sometimes of considerable size—2–3 cm. in diameter—and of extraordinary complexity.

Many Foraminifera resemble Difflugia in having a skeleton formed of sand-

grains, sponge-spicules, and other foreign bodies cemented together by a secretion from the protoplasm (Fig. 42, *1*). Some of these are formed on the imperforate type, having the protoplasm protruded from a single terminal

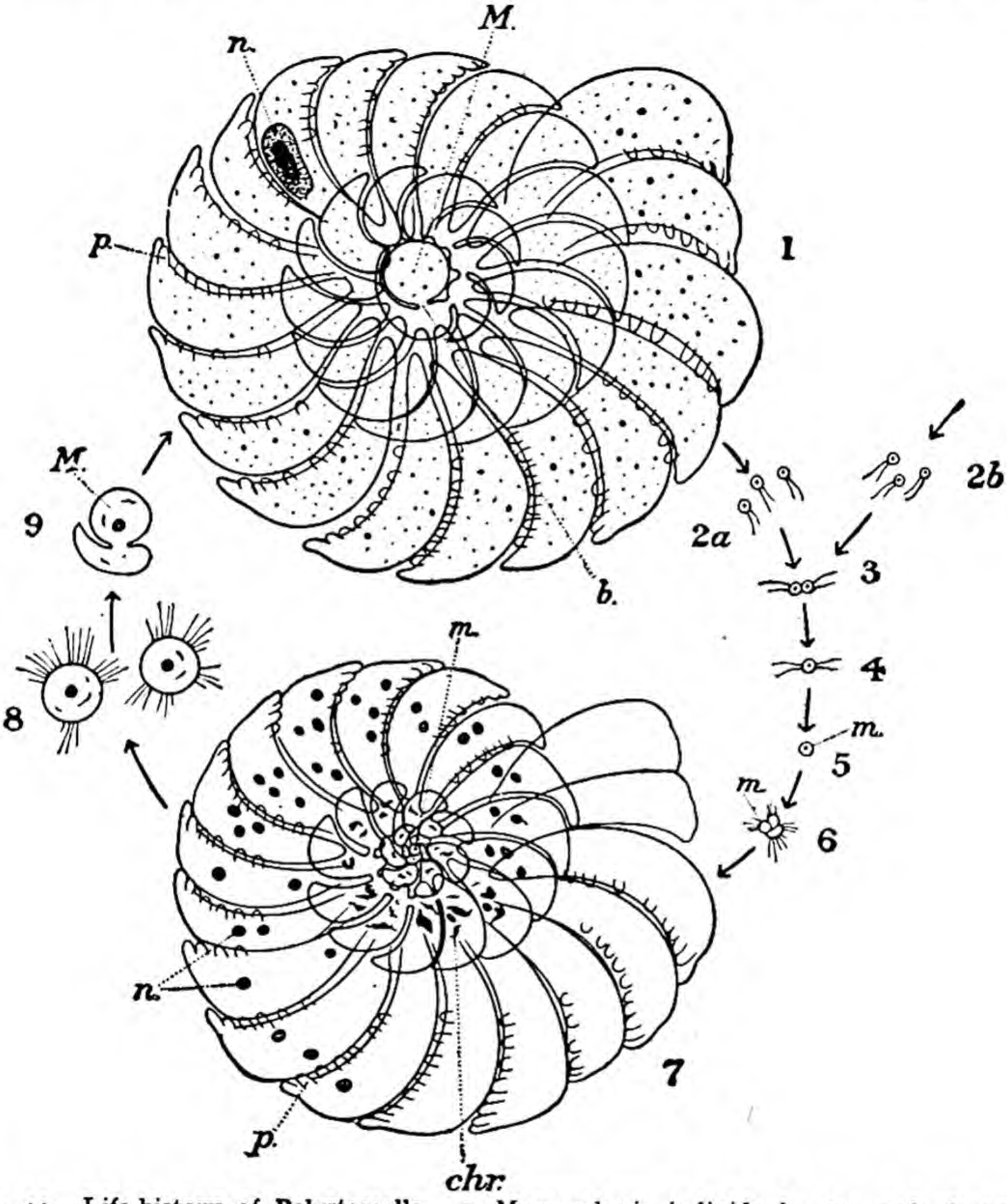


FIG. 44.—Life-history of **Polystomella.** *1*, Macrospheric individual; *2a*, and *2b*, gametes derived from two different macrospheric individuals; *3* and *4*, syngamy; *5*, zygote (central protoplasm of new microspheric individual); *6*, early stage in growth of microspheric individual; *7*, microspheric individual; *8* and *9*, young macrospheric individuals derived from *7*; *b.* protoplasmic bridge; *chr.* chromidia; *M.* central protoplasm of macrospheric individual; *m.* centroplasm of microspheric individual; *n.* nucleus; *p.* peg-like projections of cytoplasm. (From Graham Kerr's *Zoology for Medical Students* (Macmillan & Co., Ltd.).)

aperture; others on the perforate type, small pseudopods being protruded between the particles forming the shell.

In many cases the pseudopods are the only portions of protoplasm outside

the shell, whereas in Allogromia, as we saw, the shell is invested with a layer of protoplasm, and is thus in strictness an internal structure. A similar layer invests the surface in the calcareous forms with perforate shells and gives off pseudopodia in groups. In one of the calcareous forms with perforated spiral shell, called *Hastigerina* (Fig. 43), a very remarkable modification of this condition of things obtains. The shell (*sh.*) is surrounded with a mass of protoplasm (*plsm.*) many times its own diameter, and so full of vacuoles as to present a bubbly or frothy appearance. The shell itself, moreover, in this and allied forms is provided with numerous delicate, hollow, calcareous spines (*sp.*), which are only to be seen in perfect, freshly-caught specimens.

Many Foraminifera exhibit the phenomenon of **dimorphism:** the individuals of a single species occur under two distinct forms *macrospheric* and *microspheric*, differing from one another in the size of the central chamber, the shape and mode of growth of the succeeding chambers, and the number and size of the nuclei (Fig. 44).

The reproduction of Foraminifera is mainly by *multiple fission* (*merogony*), with or without copulation. The protoplasm has been observed in some to divide into minute masses which may be amœboid or may be of the nature of flagellulæ—each provided with a flagellum or a pair of flagella. The flagellulæ are gametes and copulate in pairs (syngamy). The young which develop from the zygote may form shells while still within the shell of the parent or only after becoming free. In the dimorphic Foraminifera there is evidence of the occurrence of an alternation of generations (p. 43)—the macrospheric form alternating with the microspheric, and the latter being developed as a result of a process of copulation, the former without it (alternation of sexual and asexual generations). In some Foraminifera a series of successive generations of the macrospheric type has been observed to occur before the change to a microspheric generation takes place.

Distribution.—Allogromia, Microgromia, and a few other forms are found in fresh water : one species has been found in damp earth, but the great majority of the Foraminifera are marine, some being pelagic, *i.e.*, occurring at or near the surface of the ocean, others abyssal, *i.e.*, living at great depths. In the Atlantic, large areas of the sea-bottom are covered with a grey mud called Globigerina-ooze from the vast number of Globigerinæ contained in it.

From the palæontological point of view, the Foraminifera are a very important group. Remains of their shells occur in various formations from the Ordovician period to the present day, certain rocks, such as parts of the White Chalk (Cretaceous period) and the Nummulitic limestone (Eocene) being largely made up of them.

ORDER 4.—HELIOZOA.

General Structure.—The Heliozoa are at once distinguished from the preceding groups by the character of their pseudopods, which have the form of

stiff filaments radiating outwards from the more or less globular cell-body, presenting very little movement beyond the characteristic streaming of granules, and not uniting to form networks.

One of the simplest forms is the common "Sun-animalcule," *Actinophrys sol* (Fig. 45). The body is nearly spherical, and contains a large nucleus and numerous vacuoles, one of which, near the surface, is contractile. Each of the stiff radiating pseudopods has a firm axis, apparently composed of protoplasm, which is traceable through the general protoplasm as far as the nucleus. Living organisms are devoured in much the same way as in Amœba : each is ingested

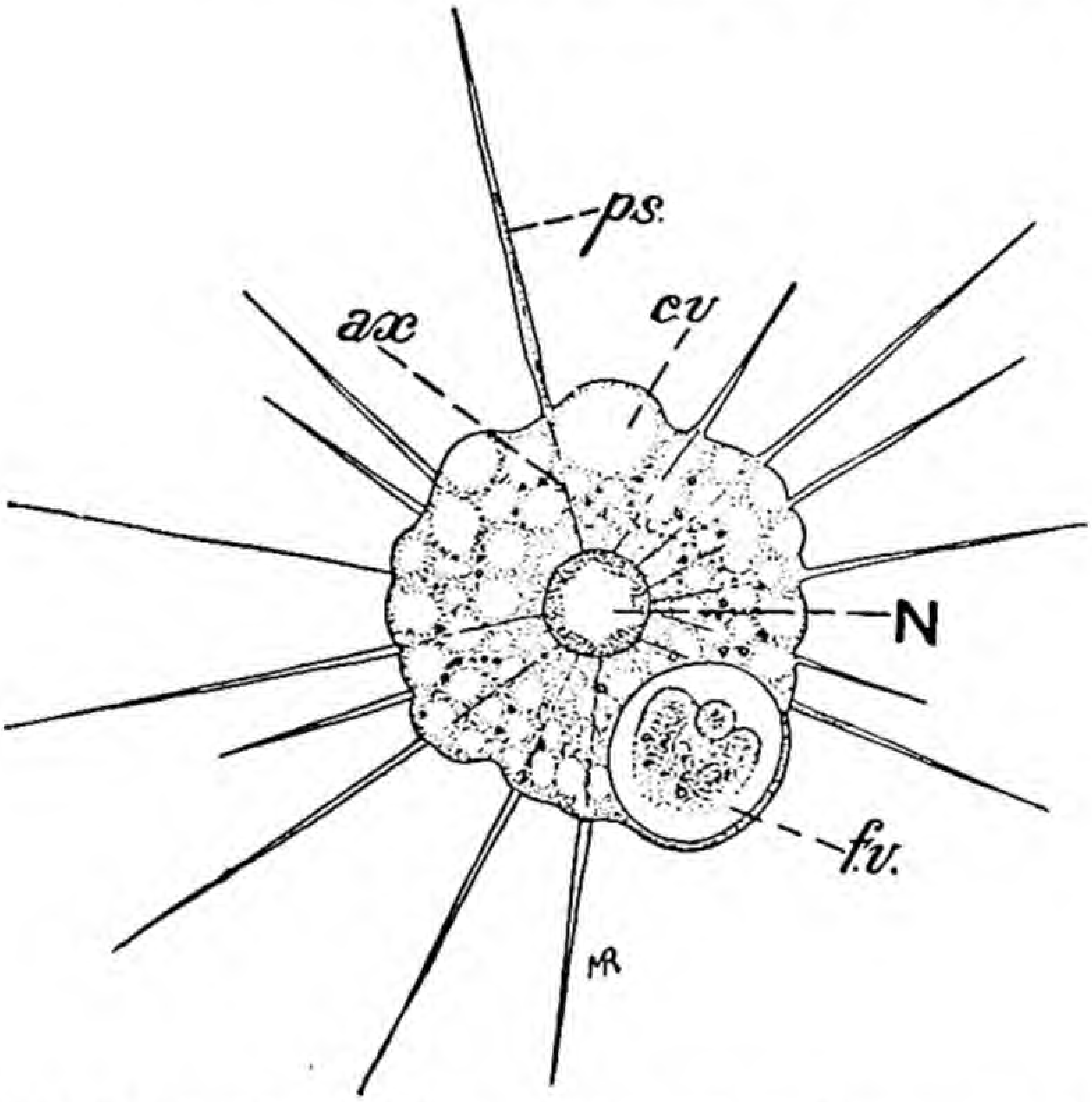


Fig. 45.—**Actinophris sol.** *ax.* axial filament; *c. v.* contractile vacuole; *f. v.* food vacuole; *N.* nucleus; *ps.* pseudopodia. (From Minchin's *Introduction to the Study of the Protozoa* (Edward Arnold), after Grenacher.)

along with a droplet of water, and is thus seen, during digestion, to lie in a definite cavity of the protoplasm, called a food-vacuole. If the organism be small, processes of the protoplasm are developed, and surround and engulf it. If it be larger, several pseudopods are applied to it, their axial fibres becoming absorbed, and their substance envelops it, enclosing it in a vacuole. The animal can fix itself by means of its pseudopods, the ends of which become viscid, and it is able to crawl slowly by their means. Sometimes it floats freely in the water, and it possesses the power of rising or sinking by some unknown means.

Actinosphærium (Fig. 46), another fresh-water form, is more complex. The protoplasm is distinctly divided into a central mass, the *medulla* or endoplasm

(*end.*) in which the vacuoles are small, and an outer layer, the *cortex* or ectoplasm (*ect.*) in which they are very large, a number of them being contractile. There are numerous nuclei (*N.*) and in some species the endosarc contains green symbiontic algæ. The axial filaments of the pseudopods are either in relation each with one of the nuclei or they converge towards a so-called central grain situated in the centre of the endosarc; in other cases they may terminate free in the protoplasm.

Many genera form **colonies.** Numerous zooids may be united by bridges of protoplasm into an open network, or the connecting bridges may be shorter and the zooids more numerous, giving the colony a more compact appearance.

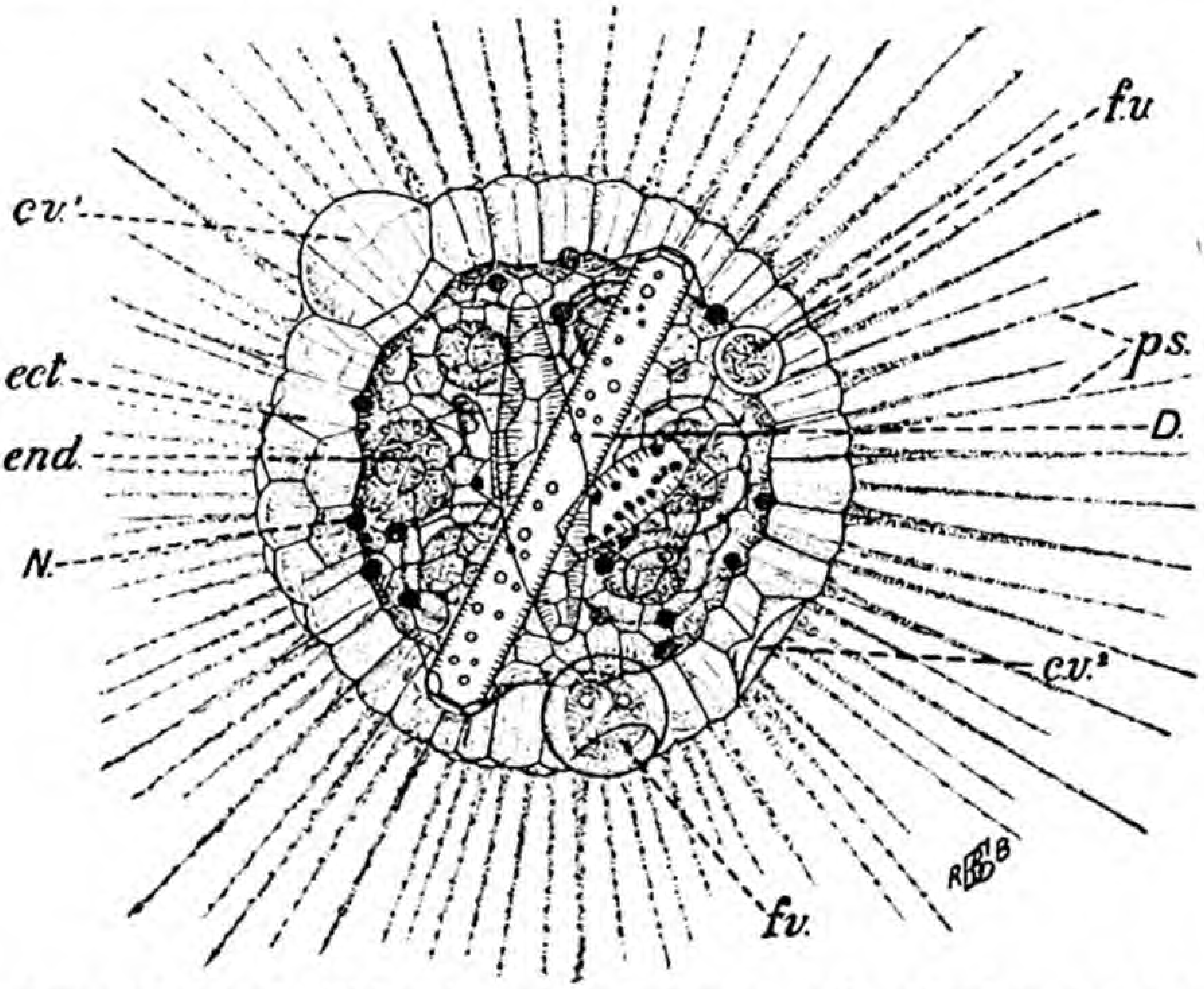


FIG. 46.—**Actinosphærium eichhornii.** *ect.* ectoplasm; *end.* endoplasm; *c. v.*¹ a contractile vacuole at its full size; *c. v.*², a contractile vacuole which has just burst; *f. v.* food vacuoles; *D.* a large diatom engulfed in the protoplasm; *N.* one of the numerous nuclei; *ps.* pseudopodia. (From Minchin's *Introduction to the Study of the Protozoa* (Edward Arnold), after Leydi.)

Transitional stages occur between the naked genera already referred to and forms with a distinct **skeleton**. Sometimes the body simply surrounds itself with a temporary gelatinous investment (Fig. 47, *2*, *g.*), in other cases it is surrounded by a capsule of loosely woven fibres through which the pseudopods pass, thus reminding us of the state of things characteristic of perforate Foraminifera. One genus has a shell formed of agglutinated sand-grains; in another (Fig. 47, *1*) the skeleton consists of loosely matted needles of silica. Lastly, in the graceful *Clathrulina* (*3*) the body is enclosed in a perforated sphere of silica, quite like the skeleton of many of the Radiolaria (p. 62).

Reproduction ordinarily takes place by binary fission; a peculiar form of

budding has been observed, and merogony also occurs, with or without encystation. Actinosphærium, for instance, encloses itself in a gelatinous cyst and undergoes multiple fission, forming numerous merozoites each enclosed in a

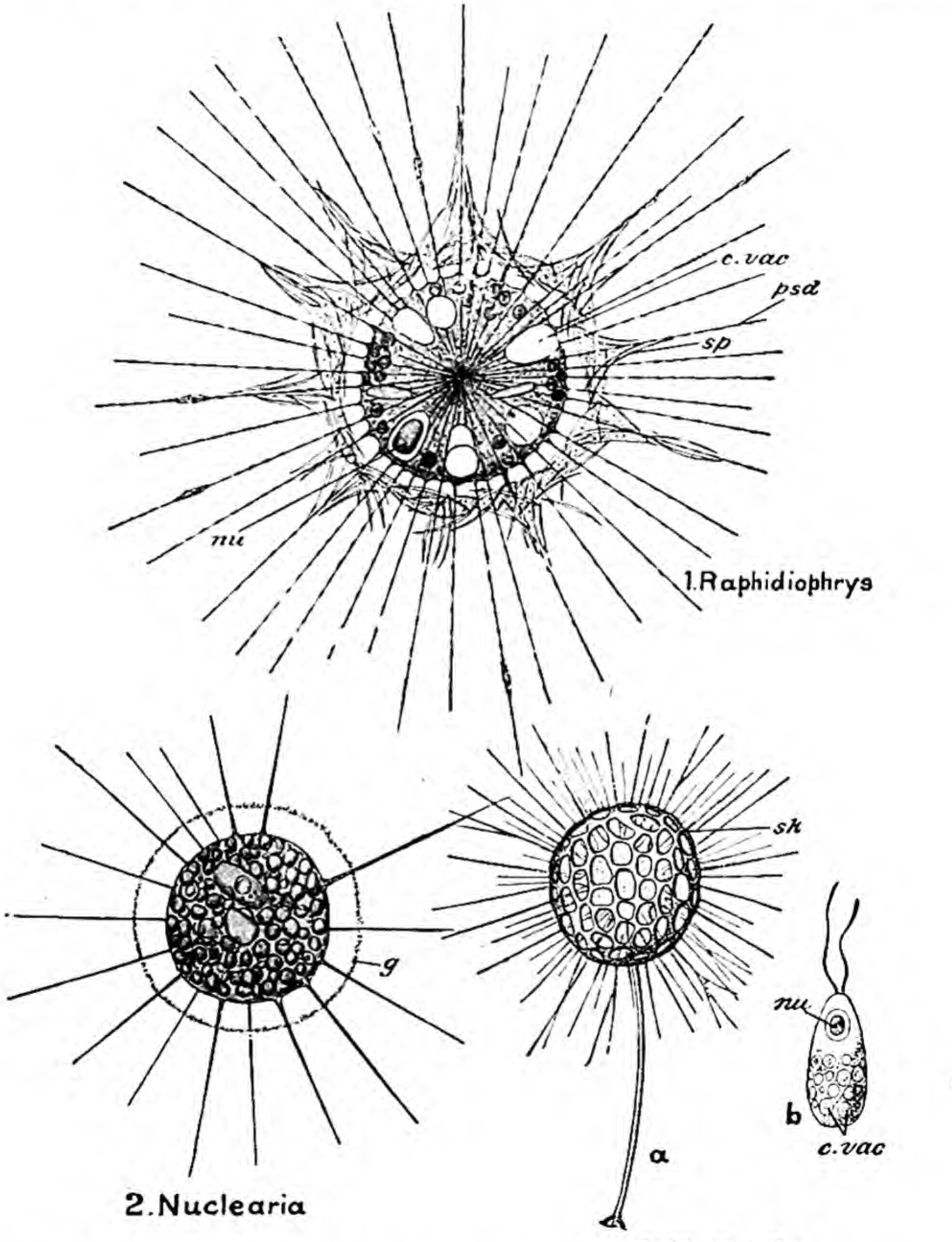


FIG. 47.—Various forms of **Heliozoa.** *3a*, the entire animal; *3b*, the flagellula; *c. vac.* contractile vacuole; *g.* gelatinous investment; *nu.* nucleus; *psd.* pseudopods; *sk.* siliceous skeleton; *sp.* spicules. (From Bütschli's *Protozoa*, after Schulze and Greeff.)

siliceous cell-wall. These "*resting spores*" remain quiescent throughout the winter, and in spring the protoplasm emerges from each and assumes the form of the ordinary active Actinosphærium. In Clathrulina merogony takes place

in the active condition, and the merozoites (Fig. 47, *3b*) are flagellulæ, each being an ovoid body provided with two flagella.

A curious process called *pædogamy* has been observed in Actinophris sol. After encystation an individual undergoes binary fission (Fig. 48, *A*, *B*, *C*), and the nuclei of the two daughter-individuals divide twice and form polar

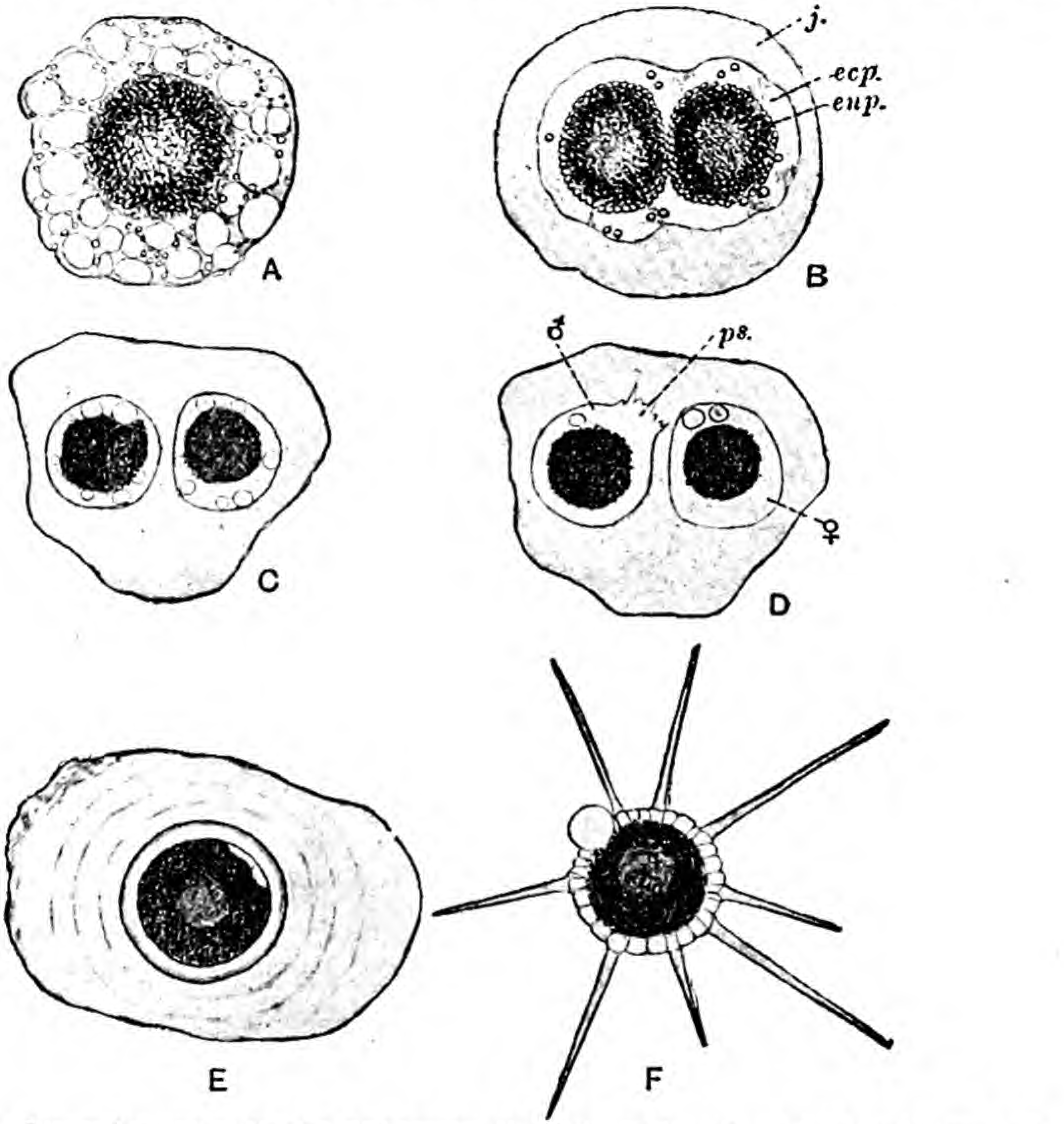


FIG. 48.—Successive stages in the pædogamy of **Actinophris sol.** *ecp.* ectoplasm; *enp.* endoplasm; *j.* jelly coat; *ps.* pseudopodium put out by the male gamete, towards the female gamete. (After Bělař.)

bodies, much in the same way as a maturing ovum (p. 21). Syngamy then takes place between the two daughter individuals, one of them, which shows pseudopodia, behaving as a male, the other as a female gamete (Fig. 48, *D*). The resulting zygote forms a thick inner cyst (Fig. 48, *E*) from which after a prolonged rest emerges a new free-living stage (Fig. 48, *F*). It is noteworthy that in this type of sexual reproduction the gametes are derived from one and

the same individual. Pædogamy has also been described in Actinosphærium, but in this case it is complicated by the fact that the animal is multinucleate.

ORDER 5.—RADIOLARIA.

The Radiolaria are a large and well-defined group of Rhizopods, noticeable, in most instances, by the presence of a siliceous skeleton of great beauty and complexity. They are all marine.

Fossil Radiolarian oozes are found as cherts in Ordovician and Carboniferous rocks, and as siliceous powders in Tertiary rocks. The latter, when used commercially, are known as "Tripoli Stone."

General Structure.—The most important characteristic of the group is the presence of a perforated membranous sac, called the *central capsule* (Fig. 49, *cent. caps.*), which lies embedded in the protoplasm, dividing it into intra-capsular (*Int. caps. pr.*) and extra-capsular (*Ext. caps. pr.*) regions. In the intra-capsular protoplasm is a large and complex nucleus (*nu.*), or sometimes many nuclei: from the extra-capsular protoplasm the pseudopods (*psd.*) are given off in the form of delicate radiating threads, which in some cases remain free, in others—*e.g.*, *Lithocircus*—anastomose freely, *i.e.*, unite to form networks. In one large section—the *Acantharia*—the pseudopodia, or some of them, contain firm axial rods similar to those in the pseudopods of the Heliozoa. There is no contractile vacuole, but in many forms the extra-capsular protoplasm contains numerous large non-contractile vacuoles, which give it the frothy or bubbly appearance noticed previously in Hastigerina. The vacuolated portion of the protoplasm has a gelatinous consistency, and is distinguished as the *calymma*. In the Acanthometridæ a gelatinous sheath formed of an extension of the calymma invests the spicules of the skeleton.

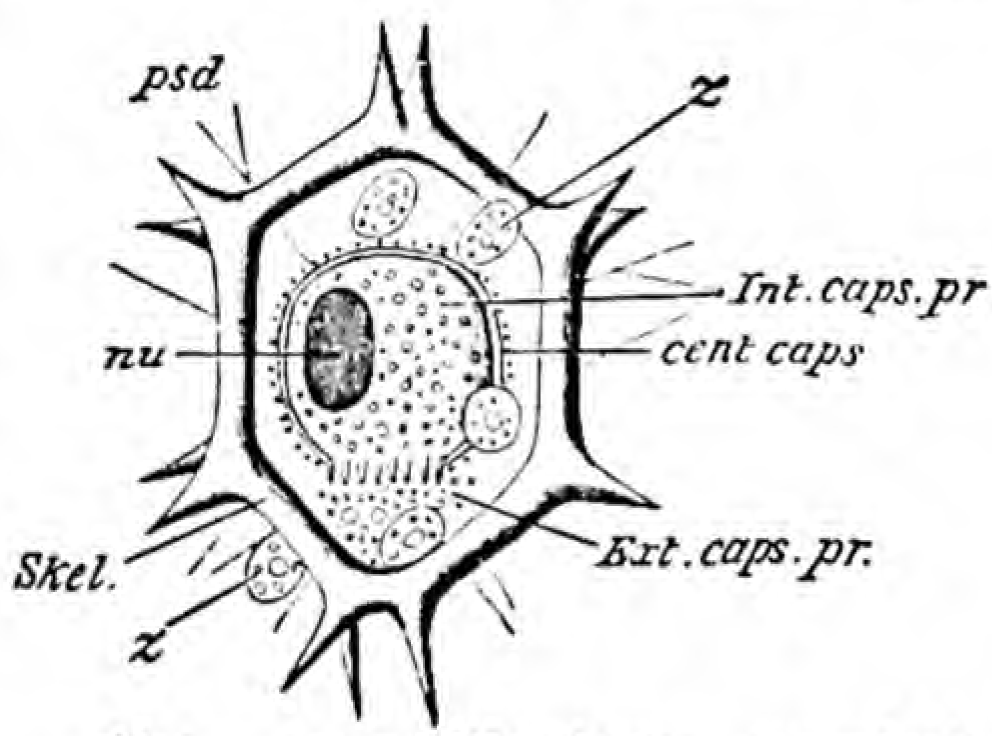


FIG. 49.—**Lithocircus annularis,** *cent. caps.* central capsule; *Ext. caps. pr.* extra-capsular protoplasm; *Int. caps. pr.* intra-capsular protoplasm; *nu.* nucleus; *psd.* pseudopods; *Skel.* skeleton; *z.* cells of Zooxanthella. (After Bütschli, from Parker's *Biology*.)

The **central capsule** may be looked upon as a chitinoid internal skeleton, reminding us of the shell of Allogromia and of the perforated calcareous shell of Hastigerina with its investment of vacuolated protoplasm. In its simplest form it is spherical and uniformly perforated with minute holes. In forms such as *Lithocircus* (Fig. 49) it is more or less conical in form, and the apertures are restricted to the flat base of the cone. Lastly, in the most complex forms (Fig. 50) the membrane of the capsule is double, and there are three apertures—a principal one having a central position and provided with a lid or *operculum*

(*op.*), and two subsidiary ones on the opposite side. In relation with the principal or lidded aperture there is found in the extra-capsular protoplasm a heap of pigmented matter called the *phæodium* (*ph.*), probably partly of the nature of excreta. The central capsule encloses, in addition to the nucleus or nuclei, oil-drops, vacuoles, crystals, and pigment.

In some genera the central capsule is the only skeletal structure present, but in most cases there is in addition a **skeleton**—mainly external—formed, as a rule, of silica, but in one subdivision of the class (the *Acantharia*) mostly of strontium sulphate, so transparent that it can only be distinguished from silica by chemical tests. The siliceous skeleton may consist of loosely woven spines,.

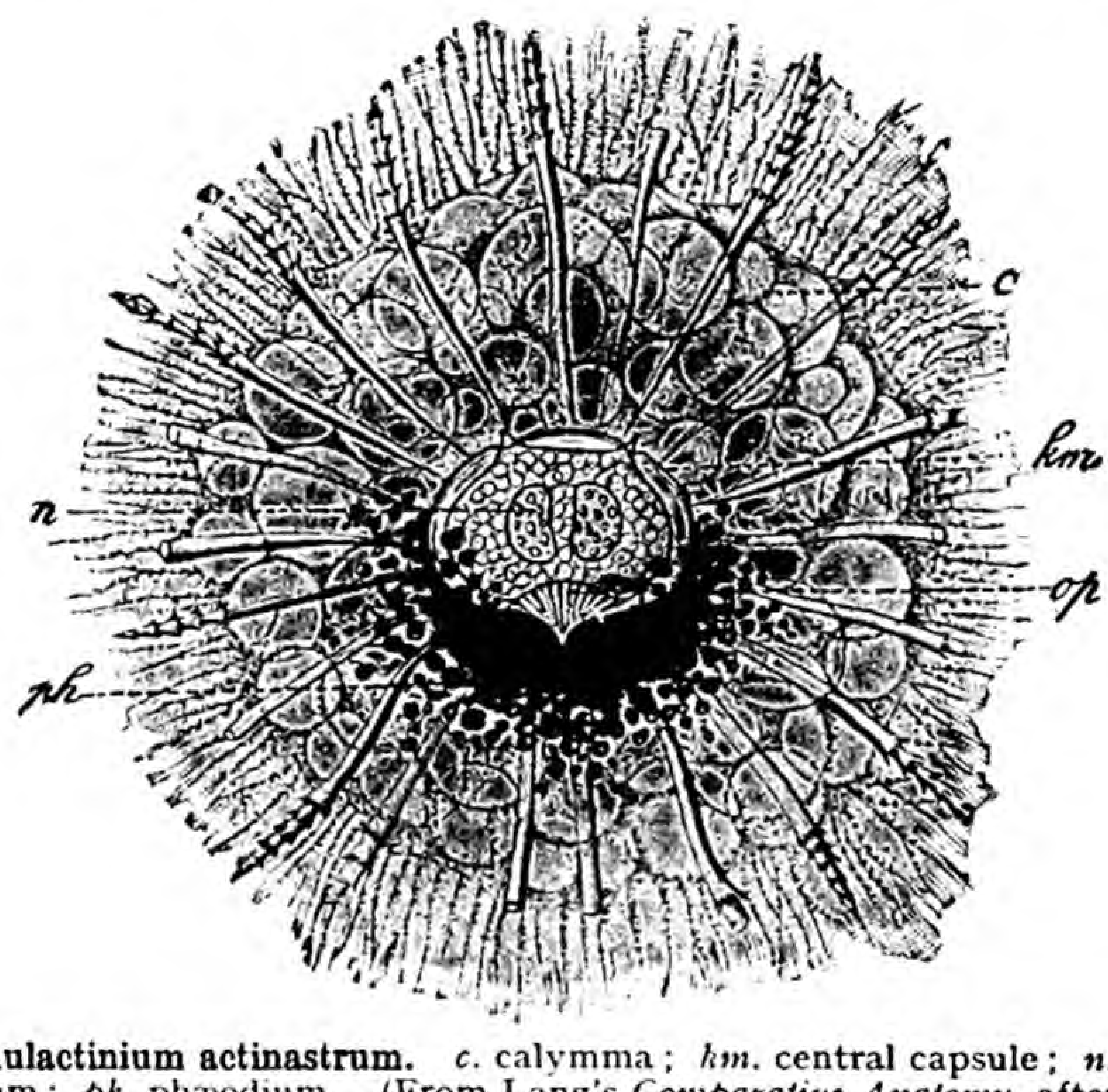


FIG. 50.—**Aulactinium actinastrum.** *c.* calymma; *km.* central capsule; *n.* nucleus; *op.* operculum; *ph.* phæodium. (From Lang's *Comparative Anatomy*, after Haeckel.)

but usually has the form of a firm framework of globular, conical, stellate, or discoid shape, frequently produced into simple or branched spines. In the Acantharia the spines frequently have inserted into them a number of contractile filaments, called myophrisks, arising from the gelatinous extra-capsular layer. A very beautiful form of skeleton is exhibited by *Actinomma* (Fig. 51), in which there are three concentric perforated spheres (*A*, *sk. 1*, *sk. 2*, *sk. 3*) connected by radiating spicules. The outer of these spheres occurs in the extra-capsular protoplasm (*B*, *ex. caps. pr.*), the middle one in the intra-capsular protoplasm, and the inner one in the nucleus (*nu.*).

Colonial forms are comparatively rare in this order, but occur in some genera by the central capsule undergoing repeated divisions while the extra-

capsular mass remains undivided. In this way is produced—in *Collozoum* for instance (Fig. 52, *A*, *B*, *C*)—a firm gelatinous mass, the calymma or vacuolated extra-capsular protoplasm (*D*, *vac.*) common to the entire colony, having

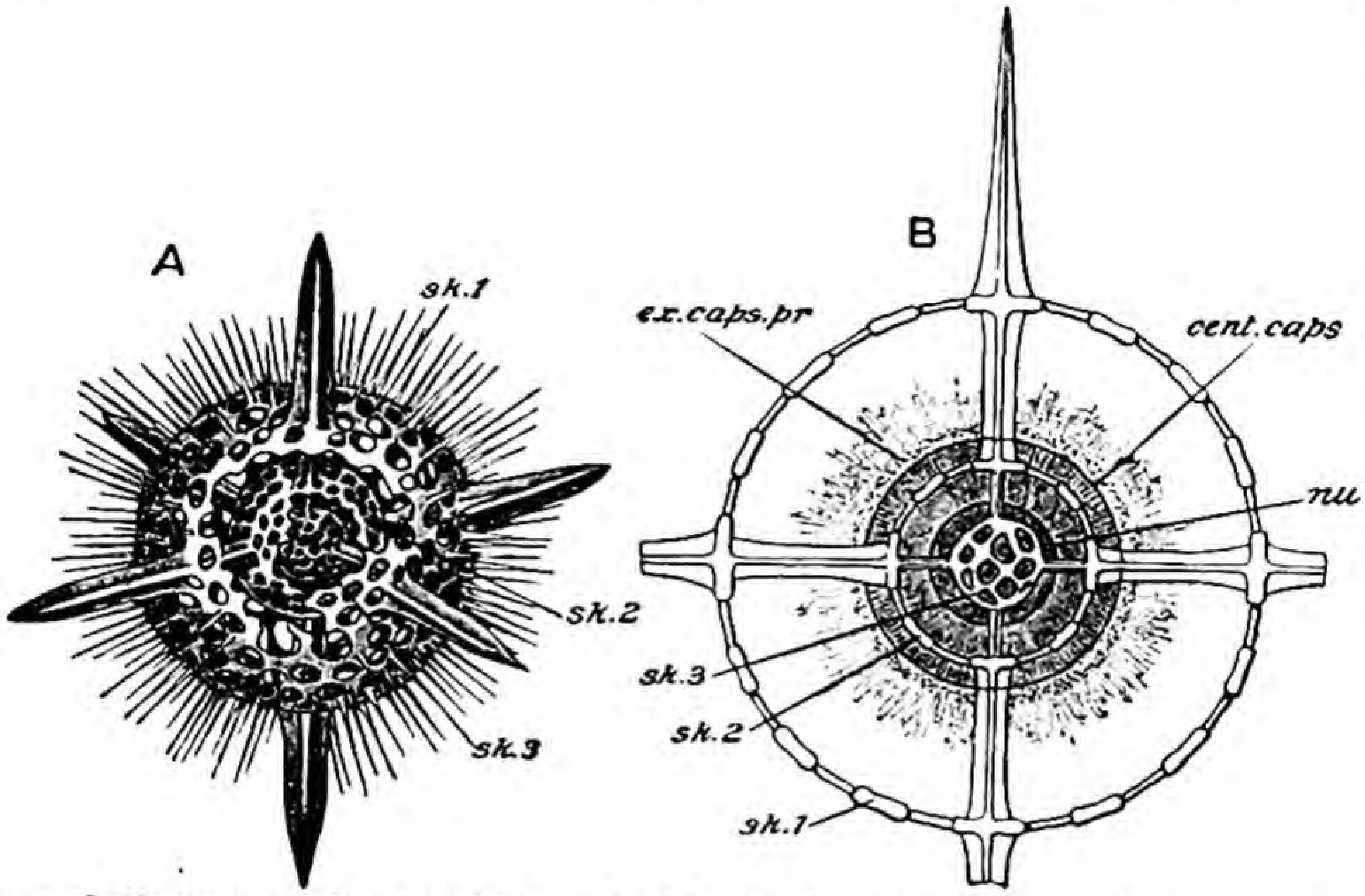


FIG. 51.—**Actinomma asteracanthion.** *A*, the shell with portions of the two outer spheres broken away; *B*, section showing the relations of the skeleton to the animal; *cent. caps.* central capsule; *ex. caps. pr.* extra-capsular protoplasm; *nu.* nucleus; *sk. 1*, outer, *sk. 2*, middle, *sk. 3*, inner sphere of skeleton. (From Bütschli's *Protozoa*, after Haeckel and Hertwig.)

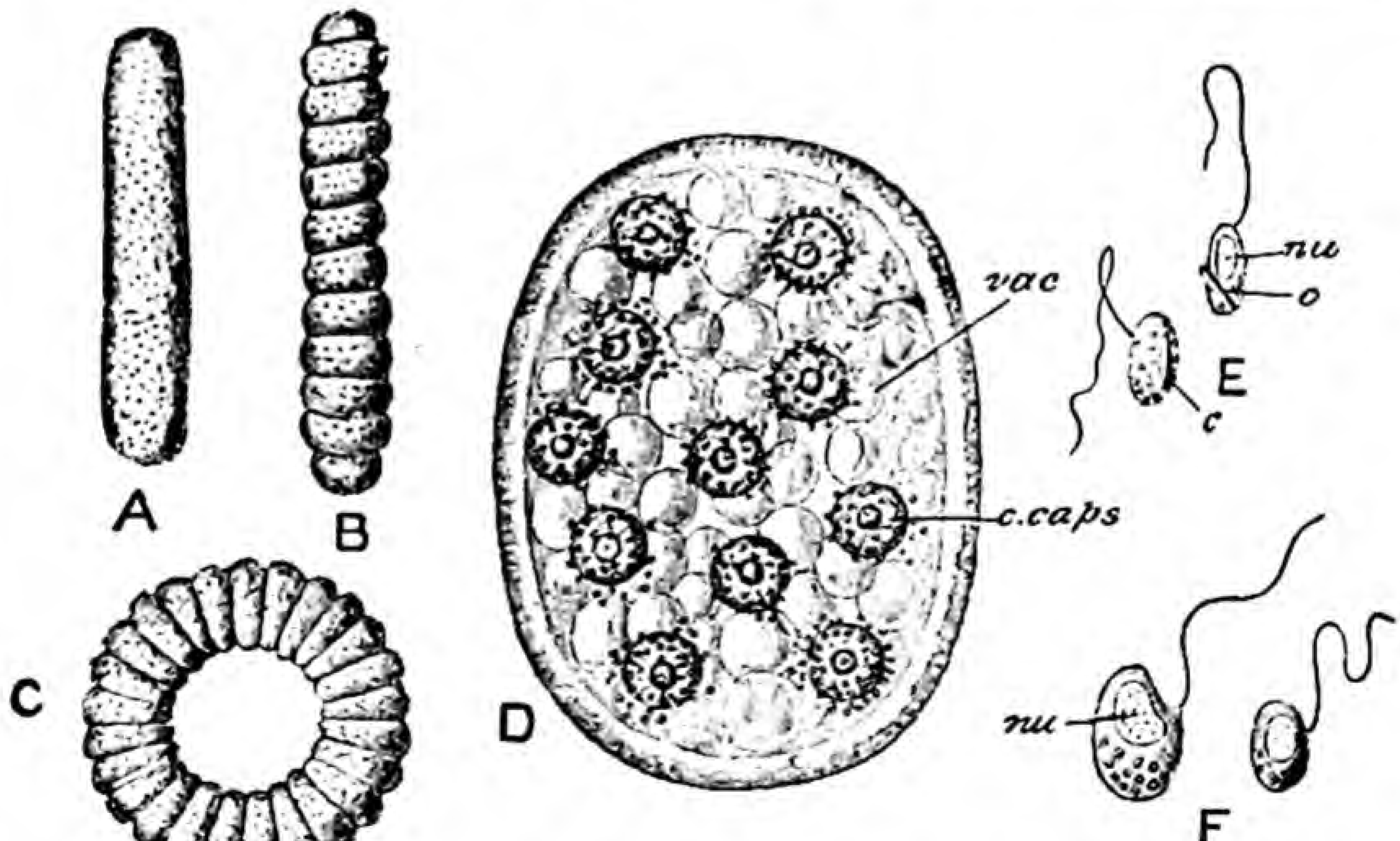


FIG. 52.—**Collozoum inerme.** *A*—*C*, three forms of the entire colony, nat. size; *D*, a small colony showing the numerous central capsules (*c. caps.*) and extra-capsular protoplasm with vacuoles (*vac.*); *E*, merozoites containing crystals (*c.*); *F*, large and small merozoite. (From Bütschli's *Protozoa*, after Hertwig and Brandt.)

embedded in it numerous central capsules (*c. caps.*) each indicating a zooid of the colony. Collozoum may attain a length of 3 or 4 cm.

Reproduction by binary fission has been observed in some cases, and may

be universal. The nucleus divides first, then the central capsule, and finally the extra-capsular protoplasm.

Merogony has been observed in Collozoum and some other genera: the intra-capsular protoplasm divides into small masses, each of which becomes a flagellula (Fig. 52, *E*, *F*) provided with either one or two flagella. In some instances all the merozoites produced are alike (*E*), and each encloses a small crystal (*c.*): in other cases (*F*)—in the same species—the merozoites are dimorphic, some being small, others large. Their development has not been traced; but in all probability they are macro- and microgametes and copulate in pairs.

Symbiosis.—In most Radiolaria there occur in the extra-capsular protoplasm minute yellow cells (Fig. 49, *z.*), each enclosed in a cell-wall, which multiply by fission independently of the Radiolarian. These are unicellular algæ named *Zooxanthellæ*. This intimate association of two organisms is called *symbiosis:* it is probably a mutually beneficial partnership, the Radiolarian supplying the Zooxanthellæ with carbon dioxide and nitrogenous waste matters, while the Zooxanthellæ give off oxygen and produce starch and other foodstuffs, some of which must make their way by diffusion into the protoplasm of the Radiolarian.

Though the occurrence of symbiotic algæ is highly characteristic of the Radiolaria, a similar association has been observed in various other Rhizopods, notably in many Foraminifera. In the Radiolarian order Acantharia, already referred to (p. 61), bodies long regarded as Zooxanthellæ occur mainly in the protoplasm of the central capsule; they have, however, been claimed not to be symbionts, but parts of the Radiolarian.

APPENDIX TO THE RHIZOPODA.

Chlamydomyxa and Labyrinthula.

Chlamydomyxa (Fig. 53), of which two species have been described, has been found living on Bog-mosses (*Sphagnum*) in Ireland and in Germany and Switzerland. It may occur either in the active or in the resting condition. In the latter (*B*, *a*, *b*, *c*) it consists of a mass of protoplasm with a number of nuclei surrounded by a laminated wall of *cellulose*—the substance characteristic of the cell-wall of the typical plant-cell. In the protoplasm are numerous non-nucleated protoplasmic bodies or chromatophores, containing chlorophyll and a yellowish-brown colouring matter in varying proportions. There are also a number of minute rounded bodies of a bluish tint probably composed of reserve food-materials. In the young condition (*a*) the resting cells are globular and microscopic, lying enclosed within the cells of the Sphagnum, but as they grow in this confined space they become elongated and irregular, and finally burst through the wall of the moss-cell, forming masses (*b*, *c*) quite visible to the naked eye. These may bud (*C*) or undergo binary fission (*D*); or the protoplasm, retreating from the cell-wall, may divide into numerous small uninucleated amœboid masses, each of which subsequently surrounds itself with a new cell-wall (*E*).

During the whole of the resting stage there is nothing to distinguish Chlamydomyxa from a plant, and it would certainly be placed among the lower Algæ if the active phase of its existence were unknown.

In the active stage (*A*) the protoplasm protrudes from the ruptured cell-wall in the form of stiff pseudopods produced into a complex network of extremely delicate filaments, which are much branched and perhaps anastomose, and may unite to form larger masses

of protoplasm at a considerable distance from the original cell. At the same time the bluish spheres (*sp.*) found in the resting stage take on a spindle shape and travel slowly along the filaments.

In one of the two known species the protoplasm entirely leaves the cyst-wall and becomes free in the water.

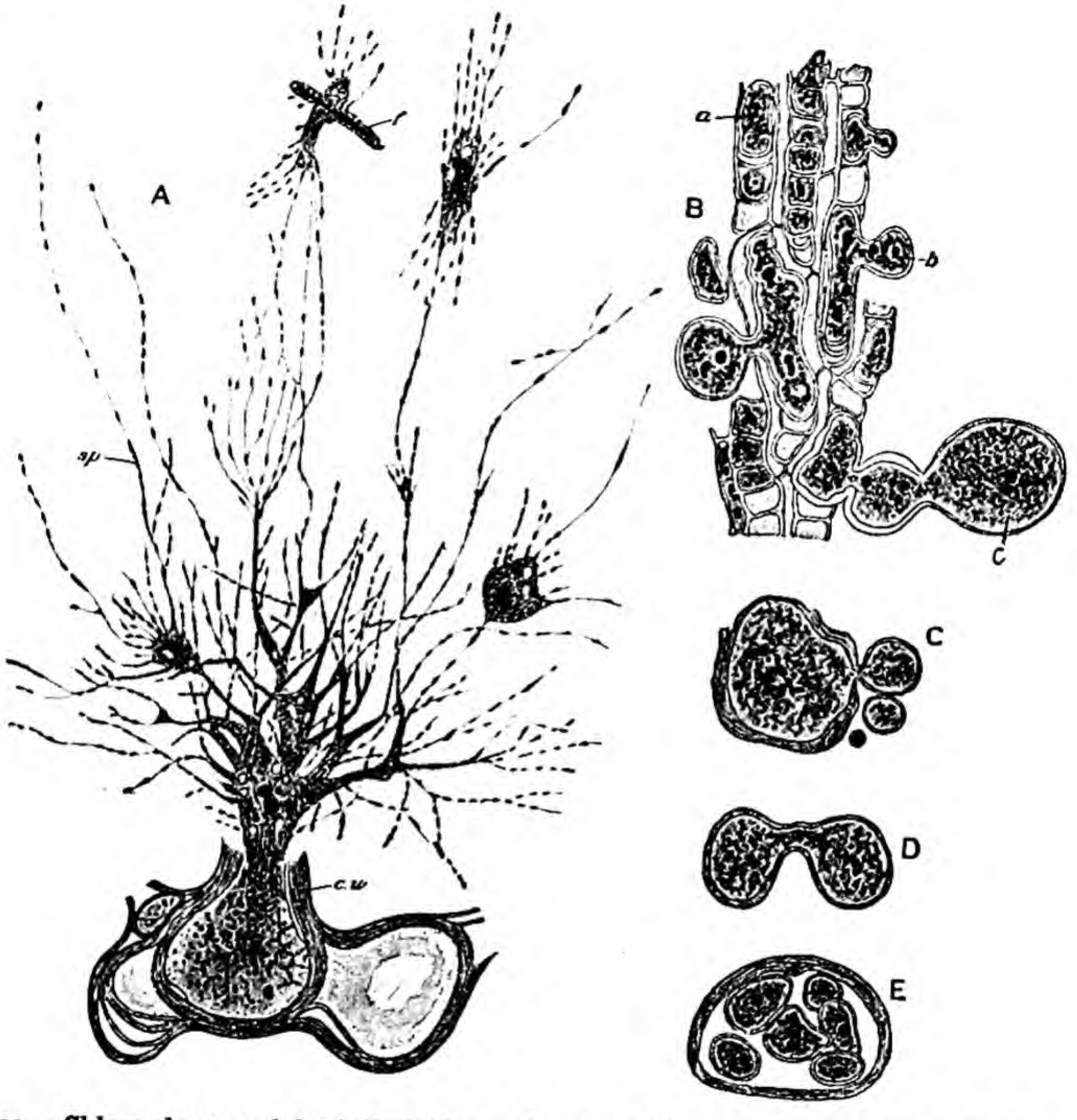


FIG. 53.—**Chlamydomyxa labyrinthuloides.** *A*, active phase; *c.w.* cell-wall; *f.* fragment of Alga ingested as food; *sp.* spindles in course of pseudopods; *B*, resting-stage—numerous individuals in the cells of a fragment of *Sphagnum*; *a*, specimen completely enclosed in cell; *b* and *c*, specimens which have emerged through the ruptured cell-wall; *C*, specimen multiplying by budding; *D*, by binary fission; *E*, by internal fission. *E* may represent a stage in spore-formation. (*A* after Archer, *B*—*E* after Geddes.)

The filaments are used to capture living organisms (*f.*) which are digested by the protoplasm surrounding them, the products of nutrition being conveyed along the network to all parts of the organism. Thus in the active condition the nutrition of Chlamydomyxa is *holozoic*, *i.e.*, strictly like that of an animal, the food consisting of living protoplasm. In the resting stage, on the other hand, nutrition is purely *holophytic*, *i.e.*, like that of an ordinary green plant, the food consisting of the carbon dioxide and various mineral salts dissolved in the water. Chlamydomyxa multiplies in the resting condition by the formation of spores, each containing two nuclei. These give rise to flagellulæ, the further history of which has not been definitely traced, but there is some evidence that copulation takes place between them.

Labyrinthula (Fig. 54), which lives parasitically on certain marine and fresh-water Algæ, in the resting stage (*B*) consists of a heap of small nucleated cells (*c.*) connected by a homogeneous substance. In the active condition (*A*) it is produced into long, delicate, stiff filaments of pseudopodial character, along which the cells (*c.*) travel, in the same manner as the spindles of Chlamydomyxa. Labyrinthula has, therefore, the character not of a single cell, but of a *cell-colony*, formed of numerous cells connected together. Chlamydomyxa, on the other hand, has the character of a single multinucleate cell. There is thus no close connection between these two aberrant forms: but both may, perhaps, best be

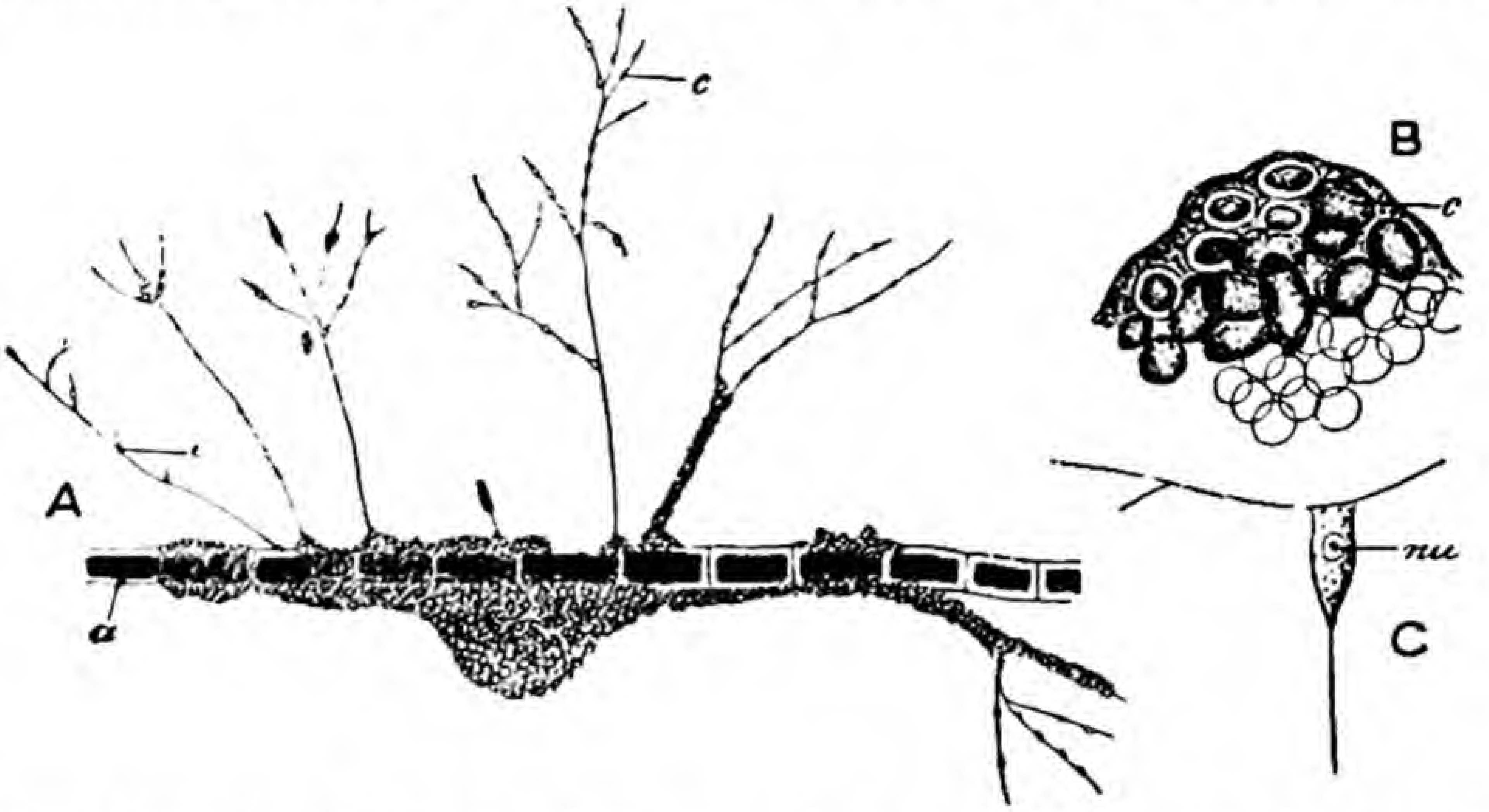


FIG. 54.—**Labyrinthula vitellina.** *A*, specimen crawling on a fragment of Alga (*a.*); *c.* cells travelling in the filaments. *B*, part of specimen in resting condition with heap of cells (*c.*); *C*, a single cell from an actively moving specimen with connecting threads; *nu.* nucleus. (From Bütschli's *Protozoa*, after Cienkowsky.)

regarded as Rhizopoda with nearer relationships to the *Foraminifera* than to any of the other orders.

An interesting organism, called *Protomyxa*, probably belongs to this group. In its plasmodial phase it consists of orange-coloured masses of protoplasm, about 1 mm. in diameter, which crawl over sea-shells by means of their long, branched pseudopods, and ingest living prey. The protoplasm becomes encysted and breaks up into naked spores, which escape from the cyst as flagellulæ, but soon become amœboid and fuse to form the plasmodium.

CLASS II.—MYCETOZOA.

1. EXAMPLE OF THE CLASS—*Didymium difforme*.

Didymium occurs as a whitish or yellow sheet of protoplasm (Fig. 55, *G*) often several centimetres across, which crawls, like a gigantic Amœba, over the surface of decaying leaves. It shows the characteristic streaming movements of protoplasm, and feeds by ingesting various organic bodies, notably the Bacilli which always occur in great numbers in decaying substances. Numerous nuclei are present.

After leading an active existence for a longer or shorter time, the protoplasm aggregates into a solid lump, surrounds itself with a cyst, and undergoes multiple fission, dividing into an immense number of minute spores. At this stage reduction of the chromosome number by one half takes place. The cyst (Fig. 55, *A*, *spg. 1*, *spg. 2*) is therefore not a mere resting capsule, like that of Amœba, but a *sporangium* or spore-case. Its wall consists of two layers, an inner of a dark purple colour and membranous texture, formed of cellulose, and an outer of a pure white hue, formed of calcium carbonate. Thus the whole sporangium, which may attain a diameter of 3 or 4 mm., resembles a minute egg.

From the inner surface of the wall of the sporangium spring a number of branched filaments of cellulose, which extend into the cavity among the spores and together constitute the *capillitium* (*B*, *cp*.).

The spores consist of nucleated masses of protoplasm surrounded by a thick cellulose wall of a dark reddish-brown colour. After a period of rest the protoplasm emerges in the form of an amœboid mass which soon becomes a flagellula (*C*), provided with a single flagellum, a nucleus (*nu*.), and a contractile vacuole (*c. vac*.). The flagellulæ move freely and ingest Bacilli (*D*, *b*.), and multiply by fission: then, after a time, they become irregular in outline, draw in the flagellum, and become amœboid (*E*), the final result being the

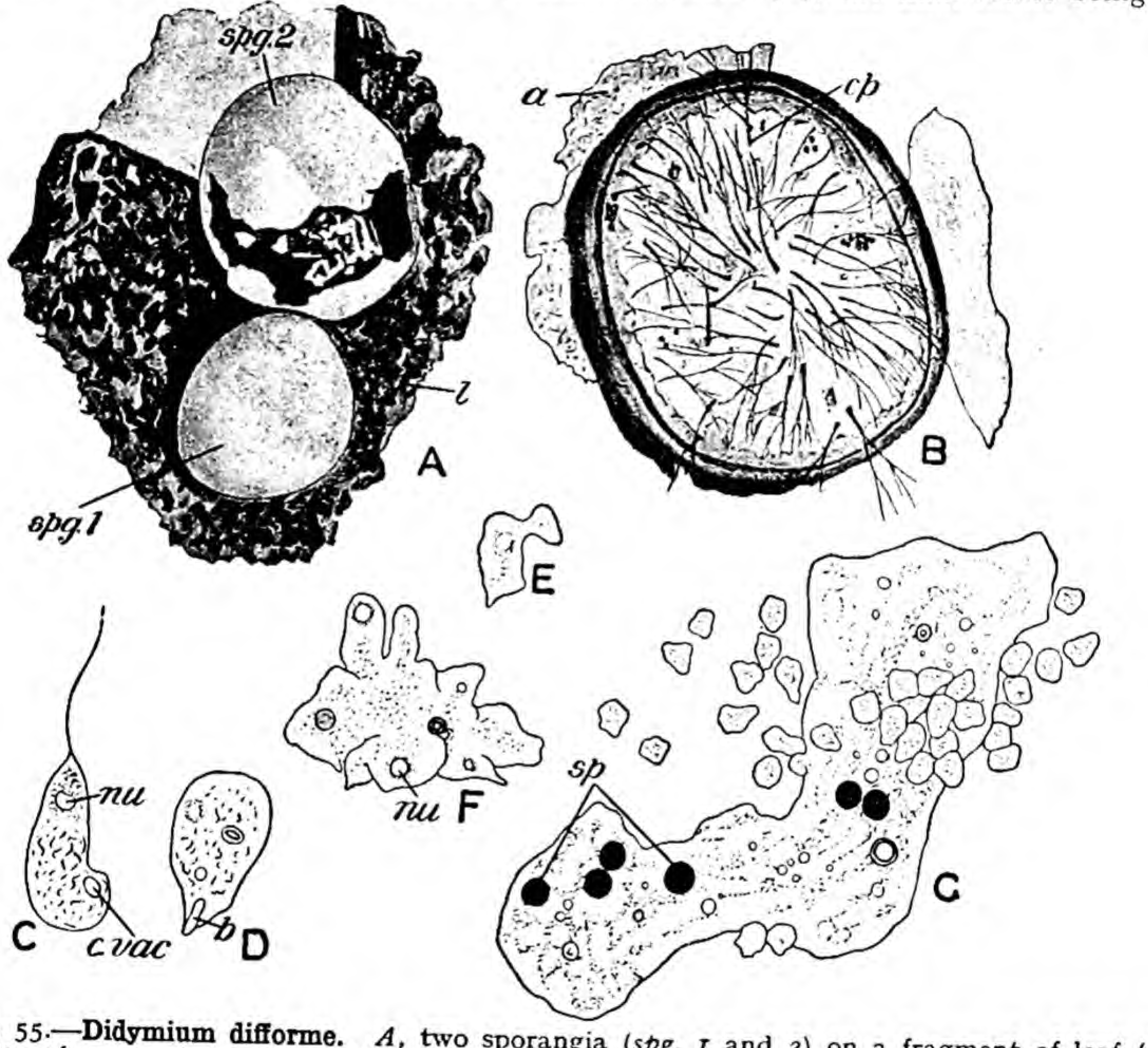


FIG. 55.—**Didymium difforme.** *A*, two sporangia (*spg. 1* and *2*) on a fragment of leaf (*l*.). *B*, section of sporangium, with ruptured outer layer (*a*.); and threads of capillitium (*cp*.). *C*, a flagellula with contractile vacuole (*c. vac*.) and nucleus (*nu*.). *D*, the same after loss of flagellum, *b*, an ingested Bacillus. *E*, an amœbula. *F*, young plasmodium. *G*, a larger plasmodium accompanied by numerous amœbulæ; *sp*. ingested spores. (After Lister.)

production of the great amœboid mass (*F*, *G*) with which we started. At which stage of the life-cycle syngamy takes place is not yet perfectly known. Didymium in its active condition is a *plasmodium*.

2. General Remarks on the Mycetozoa.

Generally considered, the Mycetozoa differ from all other Protozoa in their terrestrial habit. They are neither aquatic, like most members of the phylum, nor parasitic, like many other forms, but live habitually a sub-aërial life on decaying organic matter. They are also remarkable for their close resemblance in the structure of the sporangia and spores to certain *Fungi*, a group of parasitic or saprophytic plants in which they are often included, most works on Botany having a section on the *Myxomycetes* or "Slime-fungi," as these

organisms are then called. They are placed among animals on account of the structure and physiology of the flagellate, amœboid, and plasmodial phases, which exhibit automatic movements and ingest solid food. The Mycetozoa are sometimes included among the Rhizopoda, a course which their very peculiar reproductive processes appears to render inadvisable.

CLASS III.—MASTIGOPHORA (FLAGELLATA).

1. Example of the Class—*Euglena viridis.*

Euglena (Fig. 56) is a flagellate organism commonly found in the water of ponds and puddles, to which it imparts a green colour. The body (*A*) is about 0·1 mm. in length, is spindle-shaped, and has at the blunt anterior end a depression, the *gullet* (*A*, *B*, *gul.*), from the inner surface of which springs by two roots a single long flagellum (*fl.*). The organism is propelled through the water by the lashing movements of the flagellum, which is always directed forwards; it can also perform slow worm-like movements of contraction and expansion (*C*–*F*), but anything like the free pseudopodial movements which characterize the Rhizopoda is precluded by the presence of a membrane called pellicle which invests the body. Oblique and longitudinal lines in the outer layer of the protoplasm are due to the presence of elastic fibrils. There is a nucleus (*nc.*, *nu.*) near the centre of the body, and at the anterior end a contractile vacuole (*A*, *c. v.*), or more than one, leading into a large non-contractile space or *reservoir* (*r.*) which discharges into the gullet.

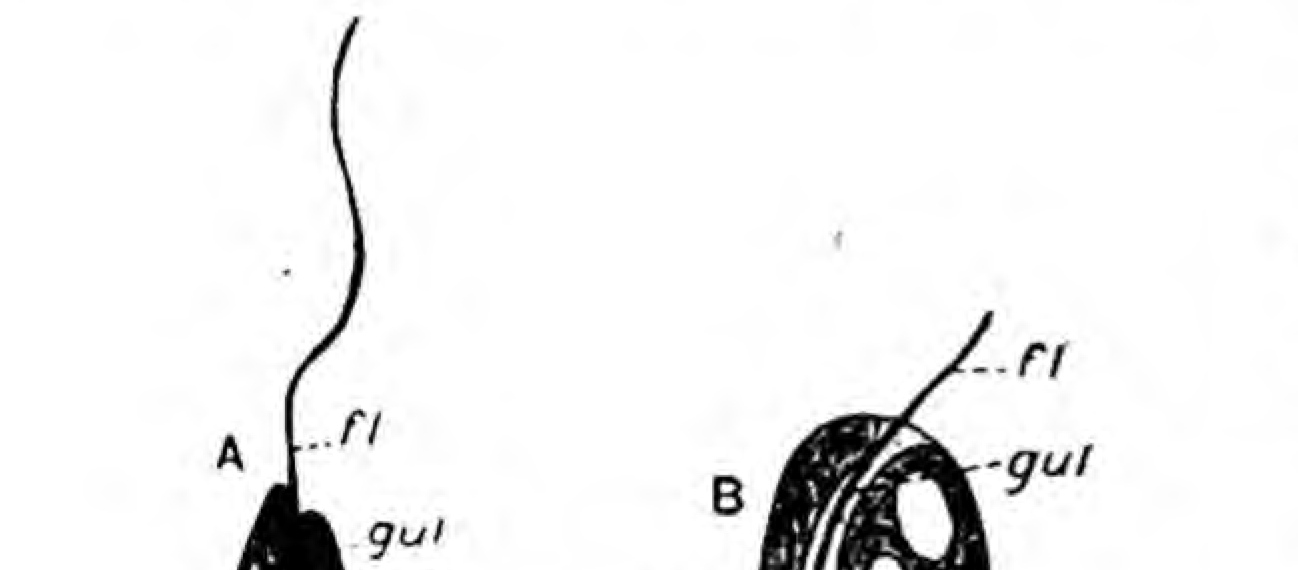


Fig. 56.—**Euglena viridis.** *A*, view of entire organism, showing details of structure (× about 1000); *B*, anterior end, to show origin of flagellum, etc. (× about 3000); *C*—*F*, four views of the living organism, showing the changes of form produced by the characteristic euglenoid movements; *G*, resting form after binary fission, showing cyst or cell-wall, nuclei, and reservoirs of the daughter-cells; *ch.* chromatophores; *c. v.* contractile vacuole; *cy.* cyst or cell-wall; *fl.* flagellum; *fl'.* thickening on flagellum; *fl''.* bifurcated base of flagellum; *gul.* gullet; *nc.*, *nu.* nucleus; *ncl.* "nucleolus"; *p.* paramylum bodies; *r.* reservoir; *st.* eye-spot or stigma. (From Parker's *Practical Zoology*:—*A*, from Doflein; *B*, from Doflein, after Wager; *C*—*G*, after Saville Kent.)

The greater part of the body is coloured green by the characteristic plant pigment, chlorophyll, and contains rod-shaped grains of

paramylum (*A*, *p*.), a carbohydrate allied to starch. In contact with the reservoir is a bright red speck, the *stigma* (*st*.), formed of an oily pigment. It has been shown to be sensitive to light. Euglena, like a typical plant, assimilates carbon by building up carbohydrates from carbon dioxide and water. In this process, which only goes on in the light, the green pigment *chlorophyll* plays an important part. Nitrogen and other elements are absorbed in the form of mineral salts in solution in the water. There is no evidence that this plant-like or *holophytic* mode of nutrition is accompanied by animal- or *holozoic* nutrition, for Euglena has not been observed to take up solid food particles through its gullet. But, in all probability, the Euglena is in large measure *saprophytic*, certain products of the decay of organic matter dissolved in the water being absorbed through the general surface.

Sometimes the active movements cease, the animal becomes quiescent, numbers of them coming together and secreting a gelatinous scum, in which they lie embedded, on the surface of the water. Each animal surrounds itself with a cyst or cell-wall of cellulose (*G*), from which, after a quiescent period, it emerges to resume active life. It is during the resting condition that reproduction takes place by the division of the body in a median plane parallel to the long axis (*G*). Under certain circumstances multiple fission takes place, and flagellulæ are produced, which, sometimes after passing through an amœboid stage, develop into the adult form.

2. Classification and General Organization.

The Mastigophora form a very extensive group, the genera and species of which show a wonderful diversity in structure and habit. The only character common to them all is the presence of one or more flagella. Some approach plants so closely as to be claimed by many botanists; others are hardly to be distinguished from Rhizopods; while others present an interesting likeness to certain peculiar cells found in Sponges.

The class is divisible into eight orders as follows :—

Order 1.—Chrysomonadina.

Small Mastigophora with one or two flagella; with a thin pellicula; often amœboid; sometimes with siliceous or calcareous skeletal structures; with yellow or brown chromatophores; nutrition mostly holophytic, sometimes saprophytic; without starch reserves, but usually with oil and characteristic reserve material, *leucosin*; abundant in freshwater and marine plancton.

Examples: *Chrysamœba* (Fig. 57, *4*), *Dinobryon* (Fig. 57, *3*); *Silicoflagellata* (Fig. 57, *1*); *Coccolithophoridæ* (Fig. 57, *2*).

Order 2.—Cryptomonadina.

Small Mastigophora with two flagella; with thin pellicula; very rarely amœboid; colourless, or with green, yellow, or brown chromatophores; nutri-

tion holophytic or saprophytic ; oil and starch as reserve material ; freshwater and marine.

Examples : *Cryptomonas* (Fig. 57, *5*), *Zooxanthellæ.*

Order 3.—Euglenoidea.

Highly organized Mastigophora with one or two flagella ; with a thick pellicula ; with mouth aperture, gullet, and complicated vacuoles ; often with green chromatophores and stigma ; holophytic nutrition prevalent ; reserve materials paramylum and oil ; freshwater.

Examples : *Euglena* (Fig. 56), *Copromonas* (Fig. 64).

Order 4.—Phytomonadina.

Mastigophora mostly with two flagella ; with a cellulose envelope ; without mouth aperture ; generally one large chromatophore and a red stigma ; nutrition mostly holophytic ; with starch reserves ; mostly freshwater.

Examples : *Hæmatococcus* (Fig. 65), *Pandorina* (Fig. 62), *Volvox* (Fig. 63).

Order 5.—Dinoflagellata.

Mastigophora having two flagella arising from about the middle of the body, one running backwards, the other encircling the body like a girdle ; body usually covered with greatly thickened cuticle or lorica with grooves for the flagella ; brown, yellow, and green chromatophores ; nutrition as a rule holophytic ; some forms phosphorescent ; marine and freshwater.

Example : *Ceratium* (Fig. 60, *2*).

Order 6.—Cystoflagellata.

Marine pelagic Mastigophora with one small flagellum, and in one case with a long striated tentacle ; body gelatinous ; with mouth opening ; holozoic nutrition ; phosphorescent. Now usually included among the Dinoflagellata.

Example : *Noctiluca* (Fig. 61).

Order 7.—Protomonadina.

Mastigophora generally of small size with one or two (in rare cases more) flagella ; with a holozoic or saprophytic mode of nutrition ; they include important parasitic forms.

Examples : *Mastigamœba* (Fig. 58, *1*), *Trypanosoma* (Fig. 58, *2*), *Choanoflagellata* (Fig. 59).

Order 8.—Polymastigina.

Mastigophora with three, four, eight, or numerous flagella ; nucleus accompanied by a characteristic cell inclusion, the so-called parabasal apparatus of unknown significance ; mostly harmless intestinal parasites or symbionts.

Examples : *Trichomonas* (Fig. 58, *3*), *Giardia* (Fig. 58, *4*).

The **cell-body** of the Mastigophora is usually ovoid or flask-shaped but may be almost globular or greatly elongated (Figs. 57, 58). Some forms have no distinct cuticle and are able to assume an amœboid form (*Chrysamœba*, Fig.

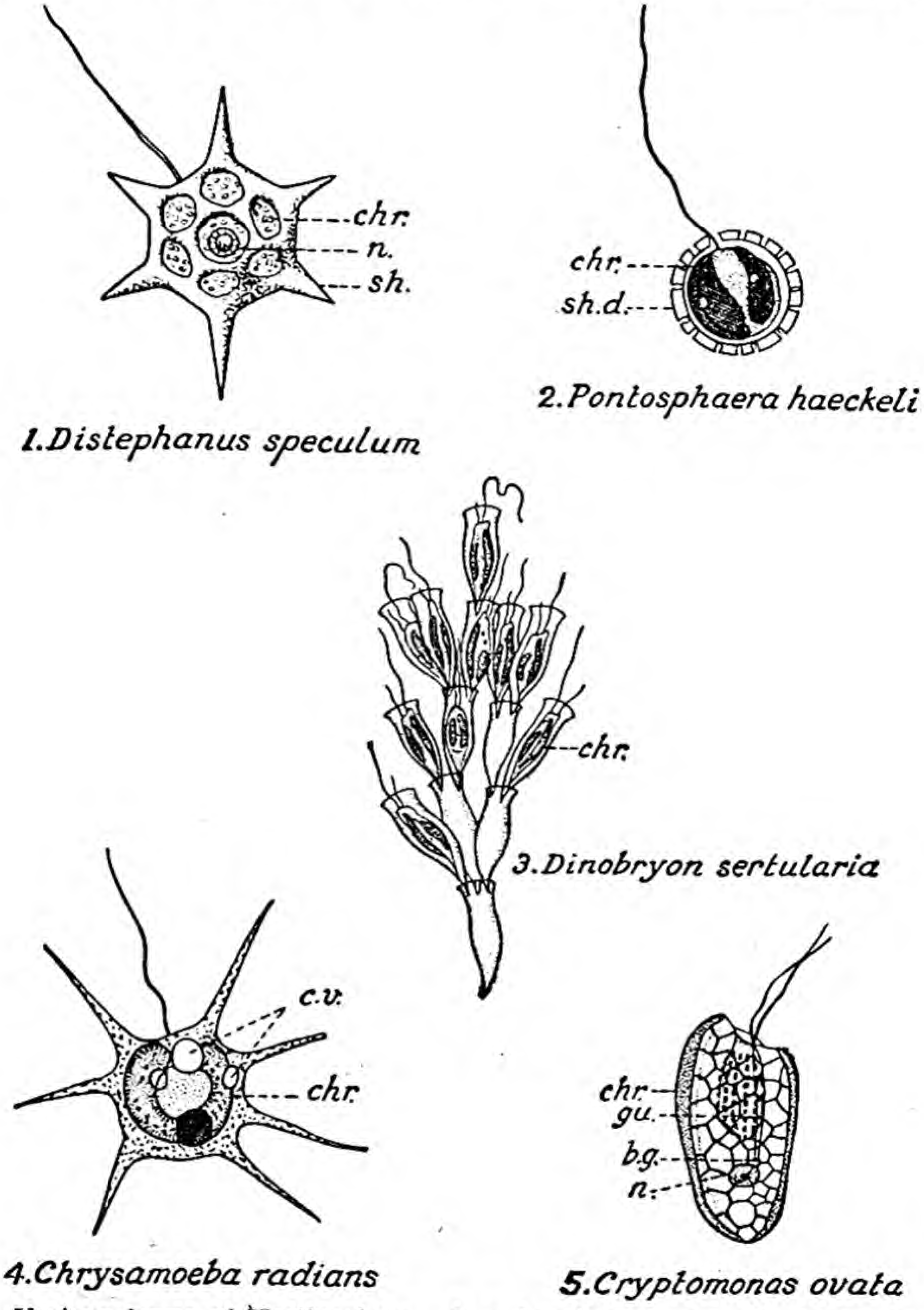


FIG. 57.—Various forms of **Mastigophora.** *b. g.* basal granules; *chr.* chromatophore; *c. v.* contractile vacuole; *gu.* gullet; *n.* nucleus; *sh.* shell; *sh. d.* shell disk (coccolith). (After various authors.)

57, *4*). The curious genus *Mastigamœba* (Fig. 58, *1*) has a permanently amœboid form, but possesses, in addition to the pseudopods, a single long flagellum. It obviously connects the Mastigophora with the Rhizopoda. Among the forms having a pellicula we find all grades from flexible cuticular structures allowing

the body to change its shape (Euglena), to rigid covers and complicated skeletal structures, as in the *Dinoflagellata* (Fig. 60), *Coccolithophoridæ* (Fig. 57, 2), and *Silicoflagellata* (Fig. 57, 1).

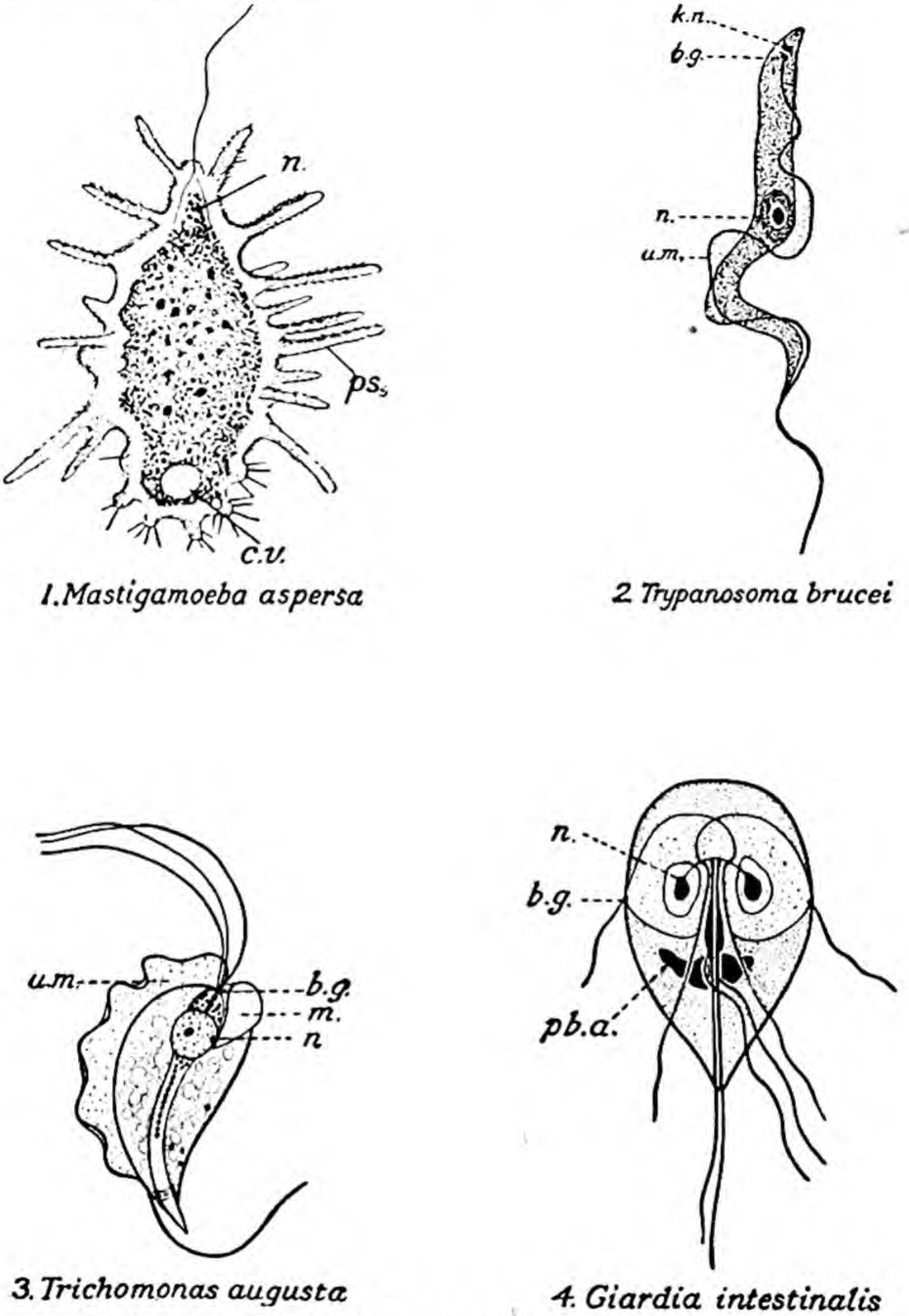


FIG. 58.—Various forms of **Mastigophora.** *b. g.* basal granule; *c. v.* contractile vacuole; *k. n.* kinetonucleus; *m.* mouth; *n.* nucleus; *pb. a.* parabasal apparatus; *ps.* pseudopods; *u. m.* undulating membrane. (After various authors.)

The number of **flagella** is subject to great variation. Frequently the flagella show a differentiation in function; in many cases in which two flagella are present only one is used in progression, the other one is trailed behind when

the animal is swimming freely, or is used to anchor it to various solid bodies. In *Trypanosoma* (Fig. 58, 2) the flagellum (or one of them if two are present) is

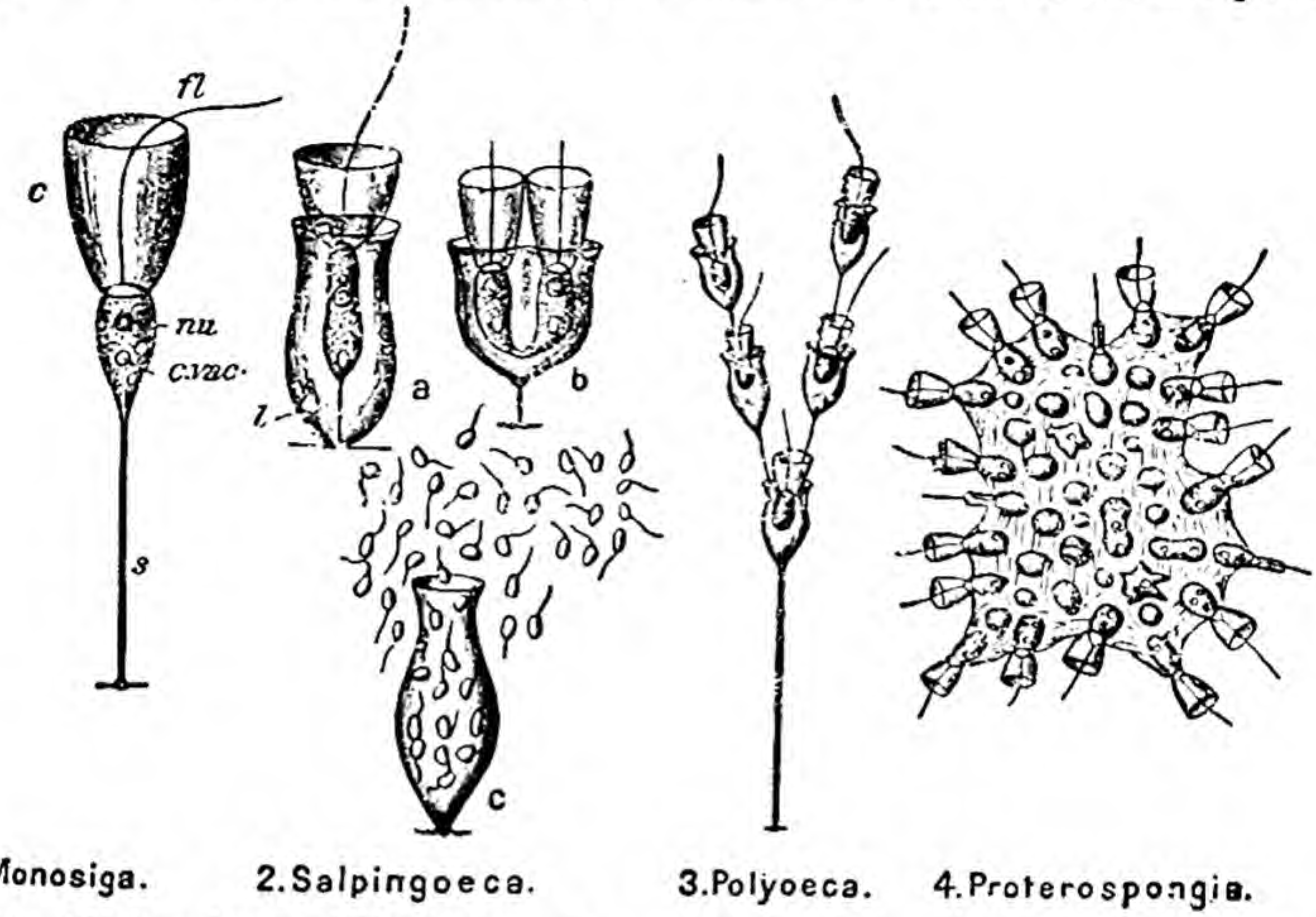


FIG. 59.—Various forms of **Choanoflagellata.** *2b* illustrates longitudinal fission; *2c*, the production of flagellulæ; *c.* collar; *c. vac.* contractile vacuole; *fl.* flagellum; *l.* lorica; *nu.* nucleus; *s.* stalk. (After Saville Kent.)

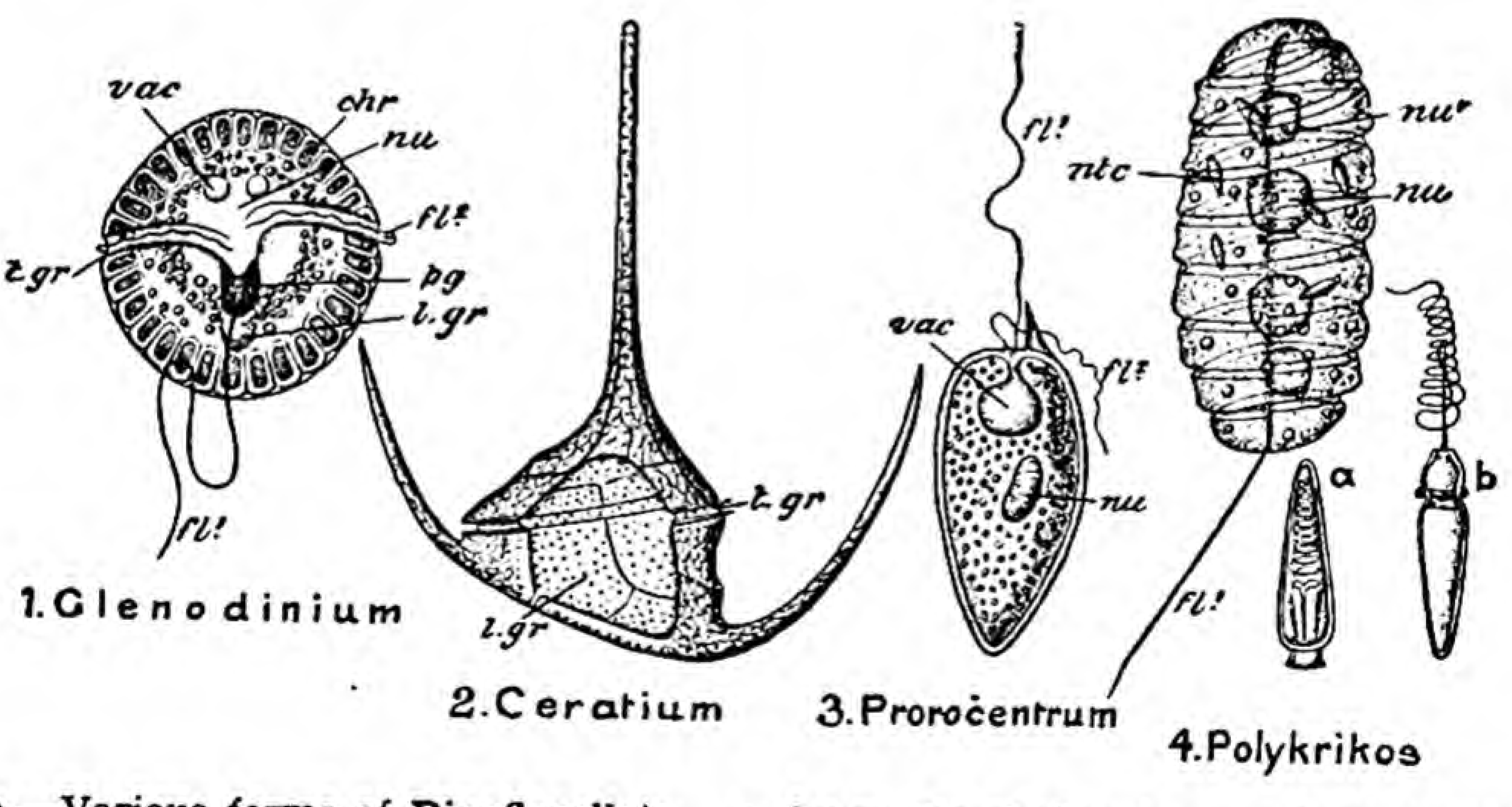


FIG. 60.—Various forms of **Dinoflagellata.** *2* shows the shell only; *4a* is an undischarged, and *b* a discharged stinging-capsule; *chr.* chromatophores; *fl. 1*, longitudinal flagellum; *fl. 2*, transverse flagellum; *l. gr.* longitudinal groove; *ntc.* stinging-capsule; *nu.*, *nu'.*, nucleus; *pg.* pigment spot; *t. gr.* transverse groove. (From Bütschli's *Protozoa*.)

attached throughout its length, or in the greater part of its length, to the edge of a wavy protoplasmic flange, the *undulating membrane*, running along the body. In the *Choanoflagellata* (Fig. 59) the single flagellum is surrounded by a

contractile protoplasmic cup or sleeve-like structure, the *collar*, which arises along a circular base-line of which the insertion of the flagellum is the centre. By the activity of the flagellum food-particles are attracted to the outside of the collar and transferred towards the collar-base by a streaming movement of the protoplasm. At the collar-base they are ingested into food-vacuoles. Thus, in the sessile forms the flagellum is principally a food-collecting organ. When temporarily set free from their substratum, the *Choanoflagellates* swim with their flagellum directed backwards. In the *Dinoflagellata* (Fig. 60) there is on the ventral surface a longitudinal groove (Fig. 60, *l. gr.*) extending along the anterior half only, and meeting a transverse groove (*t. gr.*), which is continued round the body like a girdle. From the longitudinal groove springs a long flagellum (*fl. 1*), which is directed forwards and serves as the chief organ of propulsion; a second flagellum (*fl. 2*) lies in the transverse groove, where its wave-like movements formerly caused it to be mistaken for a ring of small cilia. In *Noctiluca* (Fig. 61) the minute flagellum serves in the collecting of food only, locomotion being mostly passive. The long, stout, striated tentacle which performs twisting and lashing movements is not homologous to a flagellum. It may, however, have a locomotory function. The flagella take their origin either from the central body of the nucleus or from a so-called *basal granule*. In *Trypanosoma* the minute basal granule is in close connection with a nuclear derivative, the *kinetonucleus* (Fig. 58, *2*). Sometimes the basal granule is actually situated within the kinetonucleus, and the flagellum appears to arise directly from the latter.

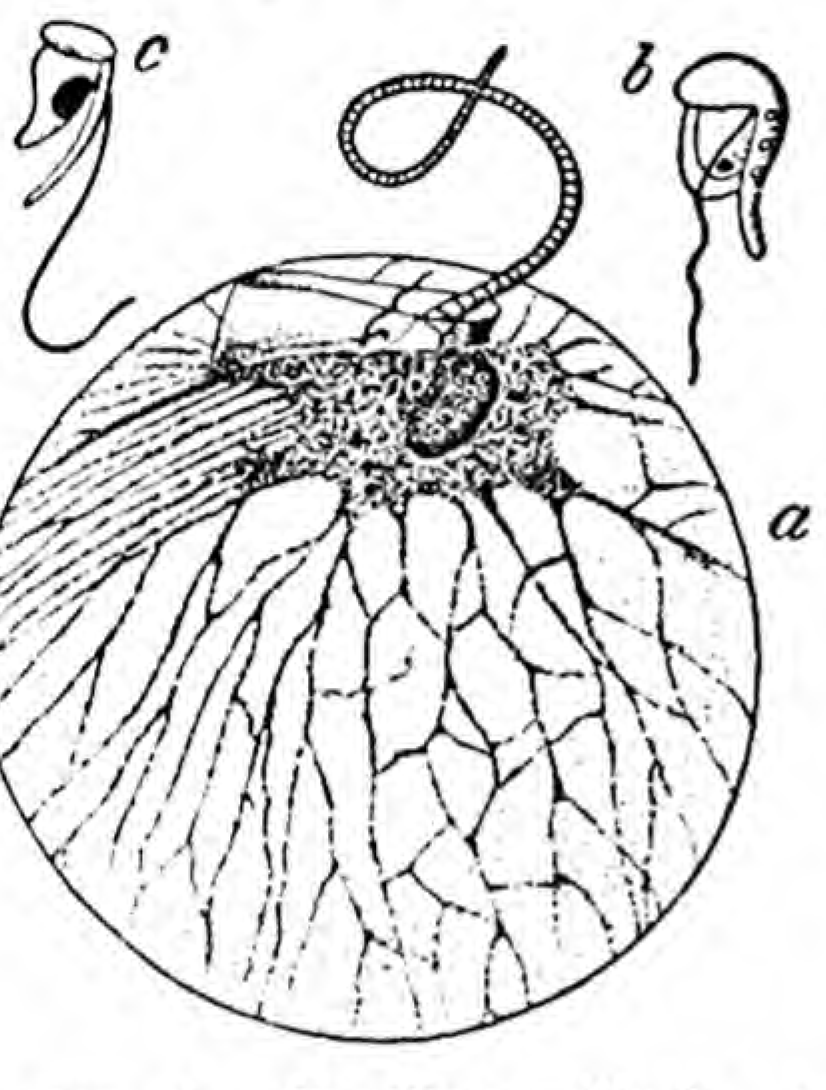


FIG. 61.—**Noctiluca miliaris.** *a*, adult animal; *b*, *c*, flagellulæ. (From Doflein-Reichenow's *Lehrbuch der Protozoenkunde* (Gustav Fischer, Jena).)

The **nuclei** differ widely in the different orders of the Mastigophora in both the arrangement of the chromatic structures and the mode of division. Besides the ordinary nucleus, we find a kinetonucleus in the Trypanosomes amongst the *Protomonadina* and a so-called parabasal apparatus in the *Polymastigina*.

Binary fission is the ordinary mode of **asexual reproduction,** and may take place in the active or in the resting position. Usually it is a longitudinal fission (Fig. 64, *a–d*), in which the nuclear division is mostly accompanied by a division of the basal granules of the flagella and by a division of the chromatophores. Transverse fission occurs in the Dinoflagellata. In some forms, especially in parasitic ones, multiple fission takes place too (Choanoflagellata, Trypanosoma, Polymastigina). Asexual reproduction frequently leads to **colony formation.** In *Dinobryon* (Fig. 57, *3*) a zooid divides within its cup, in

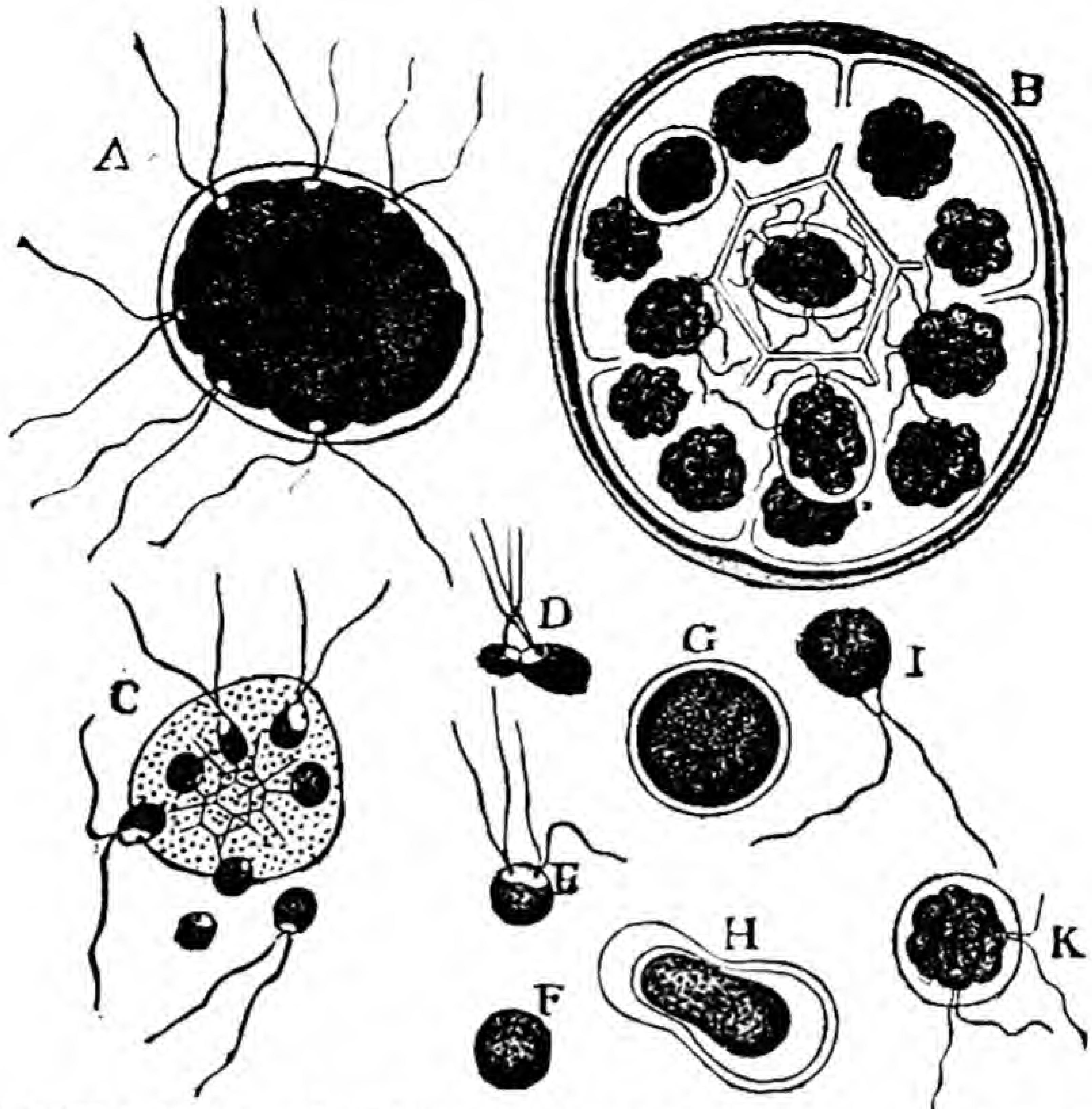


FIG. 62.—**Pandorina morum.** *A*, entire colony; *B*, asexual reproduction, each zooid dividing into a daughter-colony; *C*, liberation of gametes; *D—F*, three stages in copulation of gametes; *G*, zygote; *H—K*, development of zygote into a new colony. (From Parker's *Biology*, after Goebel.)

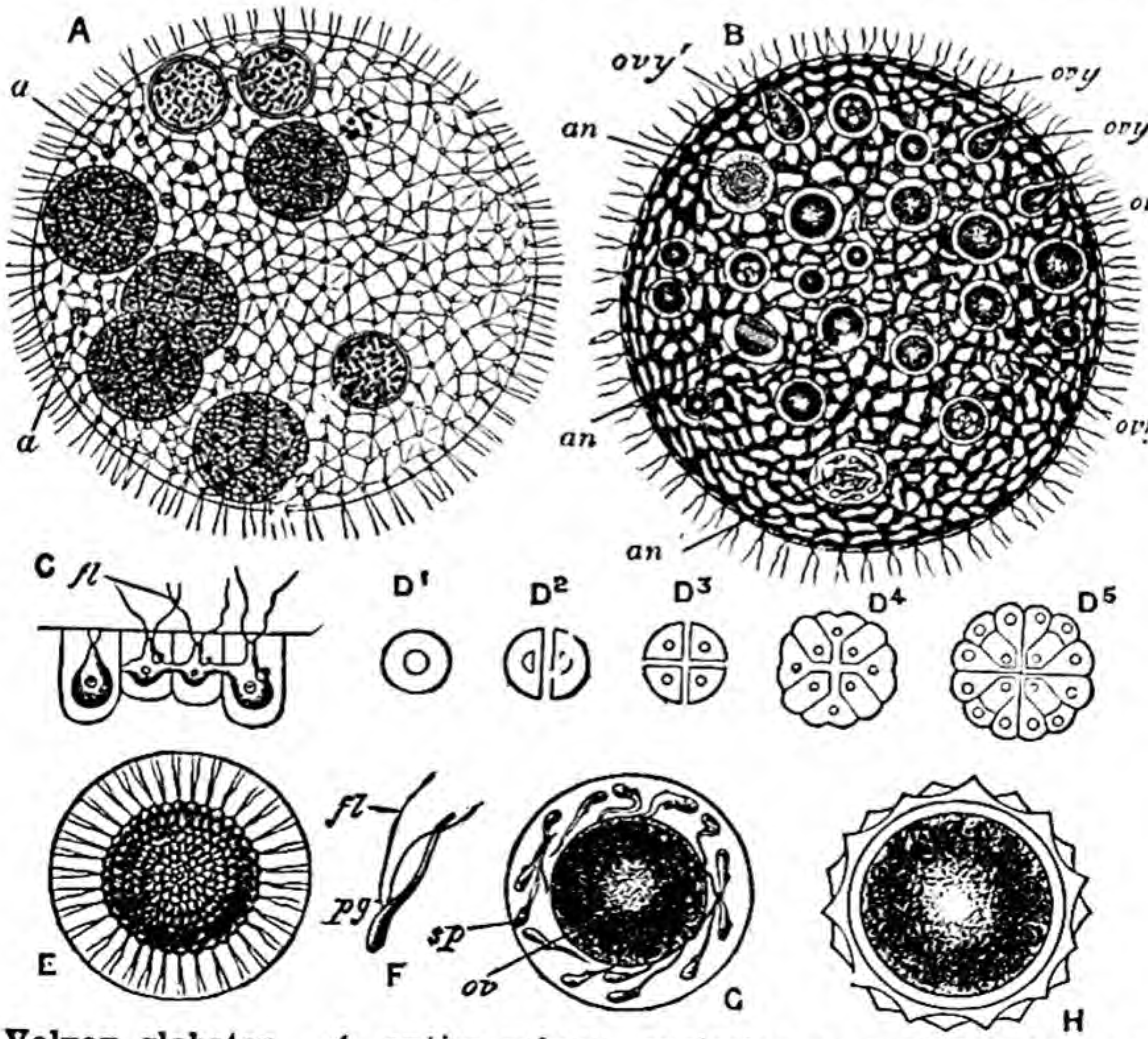


FIG. 63.—**Volvox globator.** *A*, entire colony, enclosing several daughter-colonies; *B*, the same during sexual maturity; *C*, four zooids in optical section: D^1—D^5, development of parthenogonidium; *E*, ripe antheridium; *F*, sperm; *G*, ovary containing ovum and sperms; *H*, zygote; *a*, parthenogonidia; *an*. antheridium; *fl*. flagellum; *ov*. ovum; *ovy*. ovaries; *pg*. pigment spot. (From Parker's *Biology*, after Cohn and Kirchner.)

which one of the two products of division remains; the other crawls out of the lorica, fixes itself upon its edge, and then secretes a new lorica for itself. In *Pandorina* (Fig. 62), a colonial form consisting of sixteen zooids, each of the

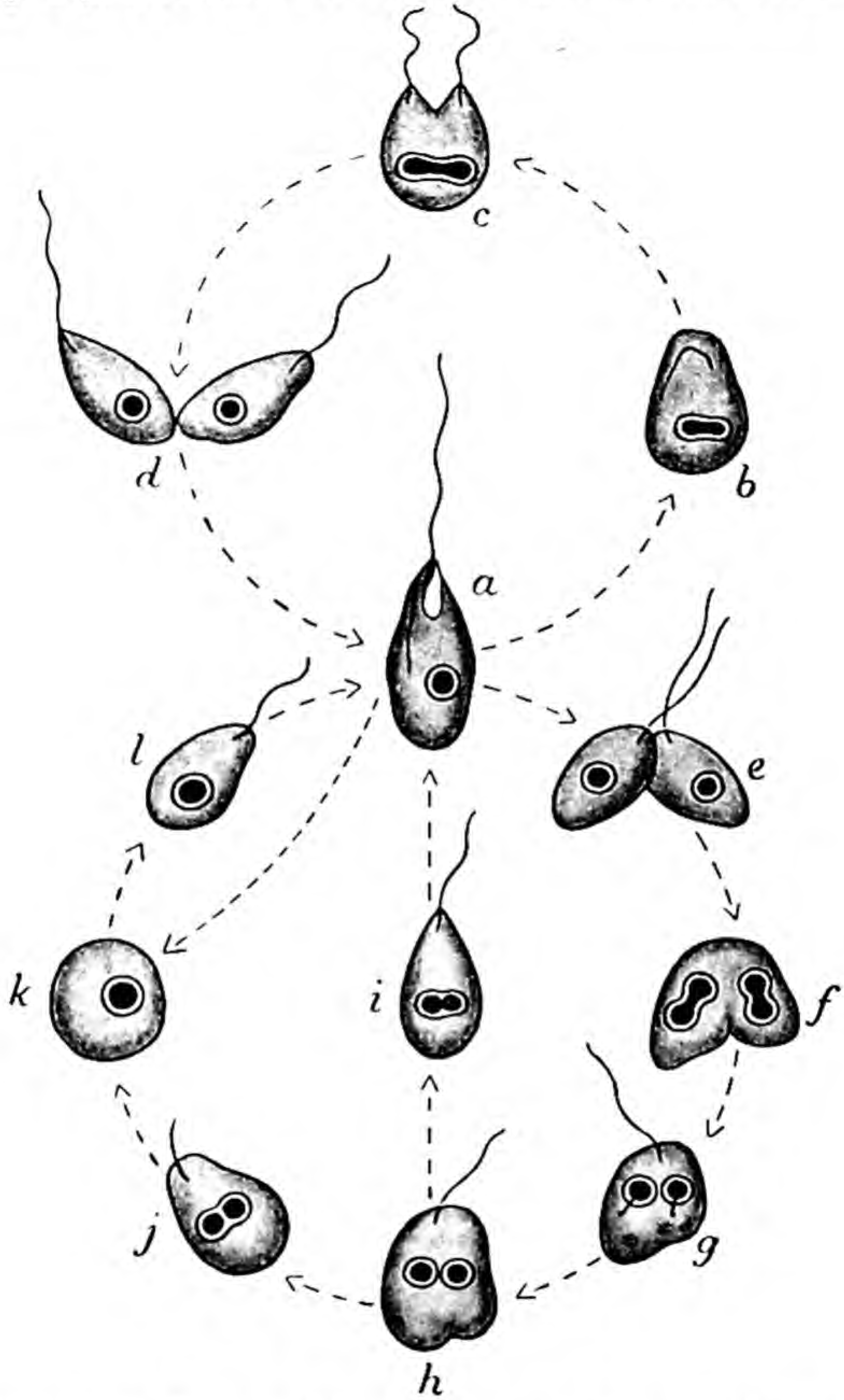


FIG. 64.—**Copromonas subtilis.** *a*, adult; *b, c, d*, stages in binary fission; *e, f, g, h, i, j*, stages in copulation with reduction (*f, g*) of the nuclei of the copulants, followed by a return to *a*, either directly (*i*) or through an encysted condition (*k*). (After Dobell.)

zooids gives rise to a daughter-colony by dividing into sixteen. The daughter-colonies are liberated by rupture of the wall of the mother-colony. In *Volvox* (Fig. 63) certain zooids, called *parthenogonidia* (*A*, *a*), have specially assigned to them the function of asexual reproduction: they divide by a process

resembling the cleavage of the egg in the higher animals (D_1–D_5) and form daughter-colonies which become detached and swim freely in the interior of the mother-colony. In the *Choanoflagellata* colonies are produced by repeated fission. In *Polyœca* (Fig. 59, *3*) the colony has a tree-like form, which may reach a high degree of complexity by repeated branching. A totally different mode of aggregation is found in *Proterospongia* (Fig. 59, *4*), in which the zooids are enclosed in a common gelatinous matrix of irregular form.

A very interesting series of stages in **sexual reproduction** is found in the various Mastigophora. In a number of cases copulation has been found to occur between ordinary individuals without any special differentiation of gametes (*hologamy*). The union of the nuclei (*karyogamy*) is always preceded in such cases by reduction divisions. *Copromonas* (Fig. 64), which occurs in the fæces of frogs, affords an example of this kind of copulation. Multiplication takes place by binary longitudinal fission (*a–d*). Copulation also takes place with reduction and karyogamy (*e–f*). This is not known to precede any special form of multiplication, but the zygote or its descendants may pass into an encysted condition (*k*) in which it is able to survive desiccation.

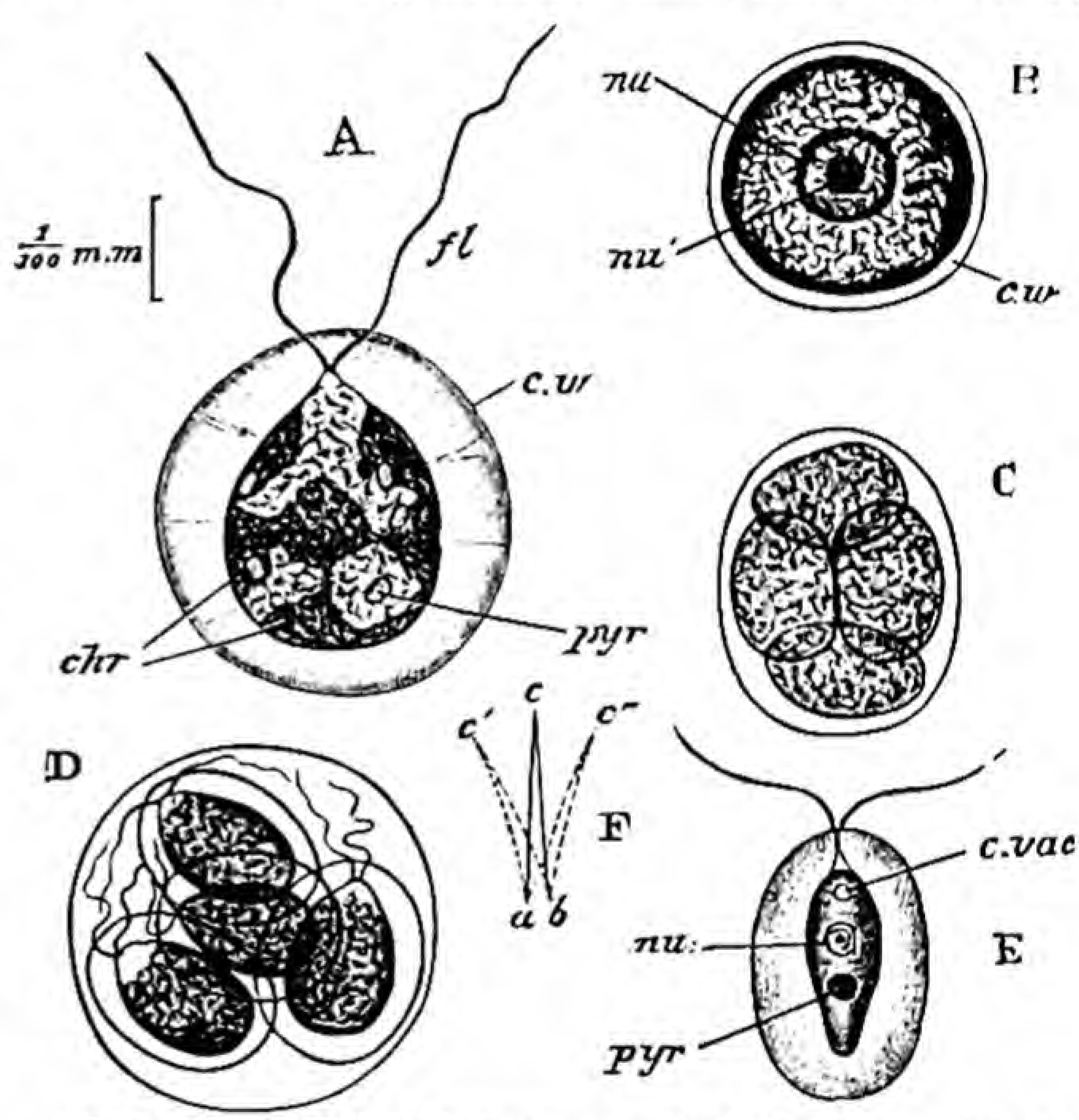


FIG. 65.—**Hæmatoccocus pluvialis.** *A*, motile stage; *B*, resting stage; *C*, *D*, two modes of fission; *E*, *Hæmatococcus lacustris*, motile stage; *F*, diagram of movements of flagellum; *chr.* chromatophores; *c. vac.* contractile vacuole; *c.w.* cell-wall; *nu.* nucleus; *nu'.* nucleolus; *pyr.* pyrenoids. (From Parker's *Biology*.)

In Pandorina (Fig. 62) the cells of the colony escape from the common gelatinous envelope (*C*) and copulate in pairs (*D*, *E*), forming a zygote (*F*, *G*), which, after a period of rest (*H*), divides and forms a new colony (*K*). In some cases the copulating cells are of two sizes, union always taking place between a large cell or *macrogamete* and a small cell or *microgamete*. In Volvox (Fig. 63) this dimorphism reaches its extreme, producing a condition of things closely resembling what we find in the higher animals. Certain of the zooids enlarge and form macrogametes (*B*, *ovy.*), others divide repeatedly and give rise to groups of microgametes(*antheridia*, *B*, *an.*, *E*, *F*) each in the form of an elongated yellow body with a red pigment-spot and two flagella. These are liberated, swim freely, and fuse with the stationary macrogamete (*G*), producing a zygote (*H*), which, after a period of rest, divides and reproduces the colony. It is

obvious that the macrogamete corresponds with the ovum of the higher animals, the microgamete with the sperm, and the zygote with the fertilized ovum (Oogamy).

In most Mastigophora **cyst formation** takes place, which either enables the

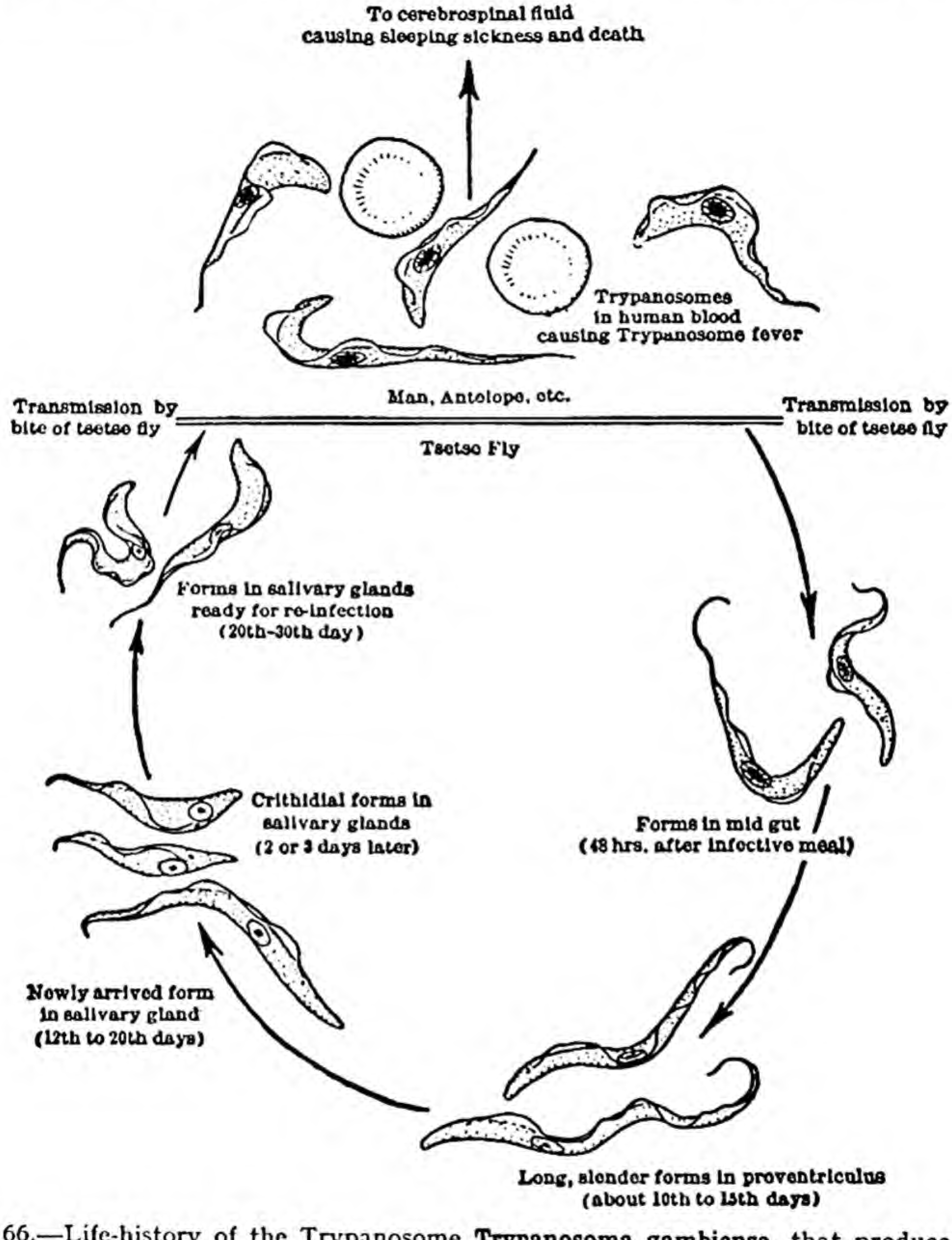


FIG. 66.—Life-history of the Trypanosome **Trypanosoma gambiense,** that produces African Sleeping Sickness in Man. (From Woodruff's *Animal Biology* (Macmillan Co.), modified after Chandler.)

forms to endure adverse external conditions or which plays an important part in asexual and sexual reproduction (Fig. 56, *G*; Fig. 65, *B–D*).

According to essential differences in their mode of life the orders of the class Mastigophora may be subdivided into two main groups. In the *first group,*

which comprises order 1–6 of our classification, holophytic nutrition and storage of polysaccharide reserve materials such as starch, paramylum, and leucosin are prevalent, although saprophytic and holozoic nutrition occur as well (*Copromonas* (Euglenoidea) and *Noctiluca* (Cystoflagellata) being entirely holozoic). Among the *Cryptomonadina* we find forms which are adapted to the symbiontic mode of life—*e.g.*, the yellow *Zooxanthellæ* living in Foraminifera, Radiolaria, and others.

The *second group* (Protomonadina and Polymastigina) contains most of the parasitic Mastigophora. Amongst them the *Trypanosomidæ* are highly interesting parasites, occurring in the blood of members of all vertebrate classes, being generally transmitted by the agency of blood-sucking invertebrates of various kinds, insects in the case of terrestrial and leeches in the case of aquatic hosts. In most cases the hosts are so well adapted to the presence of the parasite that they do not suffer any ill effects whatever. But in cases where such adaptation does not exist, serious diseases are caused by the parasite—*e.g.*, *sleeping sickness* in Man, caused by *Trypanosoma gambiense*, and *nagana* or *tsetse-fly disease* in cattle, caused by *Trypanosoma brucei*.

The life-history of *Trypanosoma gambiense* may serve as an example (Fig. 66). This species lives in the blood of African antelopes without causing any apparent discomfort to its host. When infested antelopes are bitten by the tsetse-fly *Glossina palpalis*, Trypanosomes, together with the blood of the antelope, are transferred into the gut of the insect. In the insect they undergo typical changes in shape while they migrate from the mid gut into the salivary glands. If, by a bite, transferred into the blood-stream of Man, they at first cause Trypanosome fever and subsequently, on entering the cerebro-spinal fluid, sleeping sickness leading to death.

CLASS IV.—SPOROZOA.

1. Example of the Class—*Monocystis* sp.

One of the most readily procured Sporozoa is the microscopic worm-like *Monocystis* sp. (Fig. 67, *A*), which is commonly found leading a parasitic life in the vesiculæ seminales of the common Earthworm. It is flattened, greatly elongated, pointed at both ends, and performs slow movements of expansion and contraction, reminding us of those of Euglena. In this, the *trophozoite* or adult condition, the protoplasmic body is covered with a firm cuticle, and is distinctly divided into a denser superficial portion, the *cortex*, and a central semi-fluid mass, the *medulla*. The innermost layer of the cortex consists of contractile elements or *myonemes* which act like the muscular fibres of higher animals. There is a large clear nucleus (*nu.*) with a distinct nucleolus and nuclear membrane, but the other organs of the protozoan cell-body are absent: there is

no trace of contractile vacuole, of flagella or pseudopods, of mouth or gullet. Nutrition is effected entirely by surface absorption.

Reproduction takes place by a peculiar and characteristic process of spore-formation. Two individuals come together, and become rounded off and enclosed in a common cyst (*B*), but remain separate (*syzygy*). The nucleus of each divides repeatedly, until a large number of nuclei are formed (*C*). Each of the nuclei becomes surrounded by a thin layer of protoplasm. The minute cells thus formed, after moving to and fro actively for a time, unite in pairs after

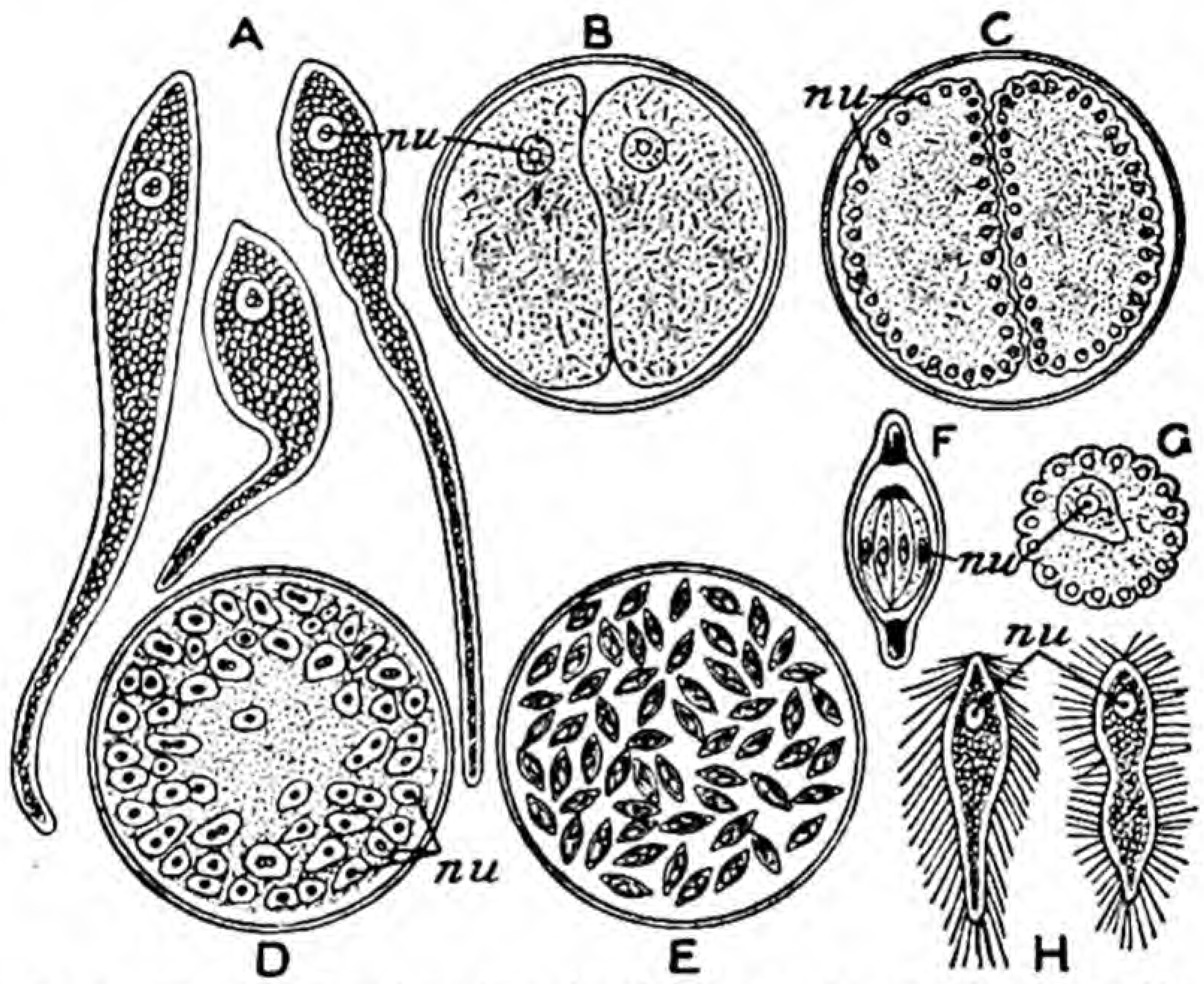


FIG. 67.—**Monocystis.** *A*, Trophozoites in different stages of contraction. *B*, encysted gametocytes. *C*, division of gametocytes into gametes. *D*, conjugation of gametes to form zygotes. *E*, Cyst enclosing ripe spores formed from the zygotes. *F*, single spore, showing the (8) sporozoites in its interior. *G*, group of developing sperm-cells of the earthworm, enclosing a sporozoite in the centre. *H*, young trophozoites still surrounded with the tails of the degenerated sperms. *nu*. nuclei. (From Parker's *Practical Zoology*.)

the substance of the two individuals has become coalescent (*D*). From each of the cells or *zygotes* that are formed by the union of two of the original small cells or *gametes*, a spore is formed, so that the cyst now comes to contain numerous small *spores* (*E*). These are spindle-shaped bodies, each enclosed in a strong chitinoid case (*F*), and thus differing in a marked manner from the naked spores of the Rhizopoda and Mastigophora. The protoplasm and nucleus of each spore then undergo fission, becoming divided generally into eight sickle-shaped bodies, the *falciform young* or *sporozoites*, which are arranged within the spore-coat somewhat like a bundle of sausages. One of the nuclear divisions is a reduction division. Thus, almost the whole life-cycle is passed in the haploid stage. In all probability the spores pass through the digestive system of a bird, pass out in its fæces, and only undergo further development if taken into the

intestine of an earthworm, when the spore-coat becomes dissolved or ruptured, and the sporozoites are set free. From the intestine they are able to migrate freely, and pass to the ciliated funnels of the male reproductive system, entering the cells of the ciliated funnels, in which they are said to live for a time as intracellular parasites, and after a time escape into the cavity of the vesicula and become lodged in the centre of one of the spherical bodies known as *sperm-morulæ*, each made up of a protoplasmic core with an investment of developing sperms (*G*). Ultimately they become free as trophozoites surrounded for a time by degenerating sperms (*H*).

2. Classification and General Organization.

The Sporozoa are exclusively parasitic, being the only group of Protozoa of which this can be said. They always multiply by spore-formation. The class is divisible into the following sub-classes and orders :—

Sub-class I.—Telosporidia.

Sporozoa in which the adult trophozoite is uninuclear ; simple spore cases containing several sporozoites.

Order 1.—Gregarinida.

Telosporidia in which the trophozoite is free and motile.
Examples : *Monocystis* (Fig. 67), *Gregarina* (Fig. 68), *Schizocystis* (Fig. 69).

Order 2.—Coccidia.

Telosporidia in which the trophozoite is a minute intra-cellular parasite.
Example : *Eimeria* (Fig. 70).

Order 3.—Hæmosporidia.

Telosporidia in which the trophozoite is amœboid, and lives as a parasite in the coloured blood-corpuscles of Vertebrates.
Example : *Plasmodium* (Fig. 71).

Sub-Class II.—Neosporidia.

Sporozoa in which the adult trophozoite is multinuclear ; with complex spore cases, generally containing a single germ.

Order 1.—Myxosporidia.

Neosporidia in which the trophozoite is amœboid, but not intracellular.
Examples : *Myxidium* (Fig. 72), *Nosema*.

Order 2.—Sarcosporidia.

Elongated Neosporidia usually found in muscle.
Example : *Sarcocystis* (Fig. 73).

Sub-class I.—Telosporidia.

ORDER I.—GREGARINIDA.

Monocystis is one of the simpler representatives of the Gregarinida as regards both structure and life-history. The structure of the adult or trophozoite is complicated in *Gregarina* (Fig. 68) and allied genera by the division of the body into two parts, *protomerite* in front and *deutomerite* behind, by a sort of transverse septum formed by an ingrowth of the layer of myonemes—the nucleus being usually situated in the deutomerite. Sometimes the protomerite is produced in front into a process ending in a rounded enlargement the

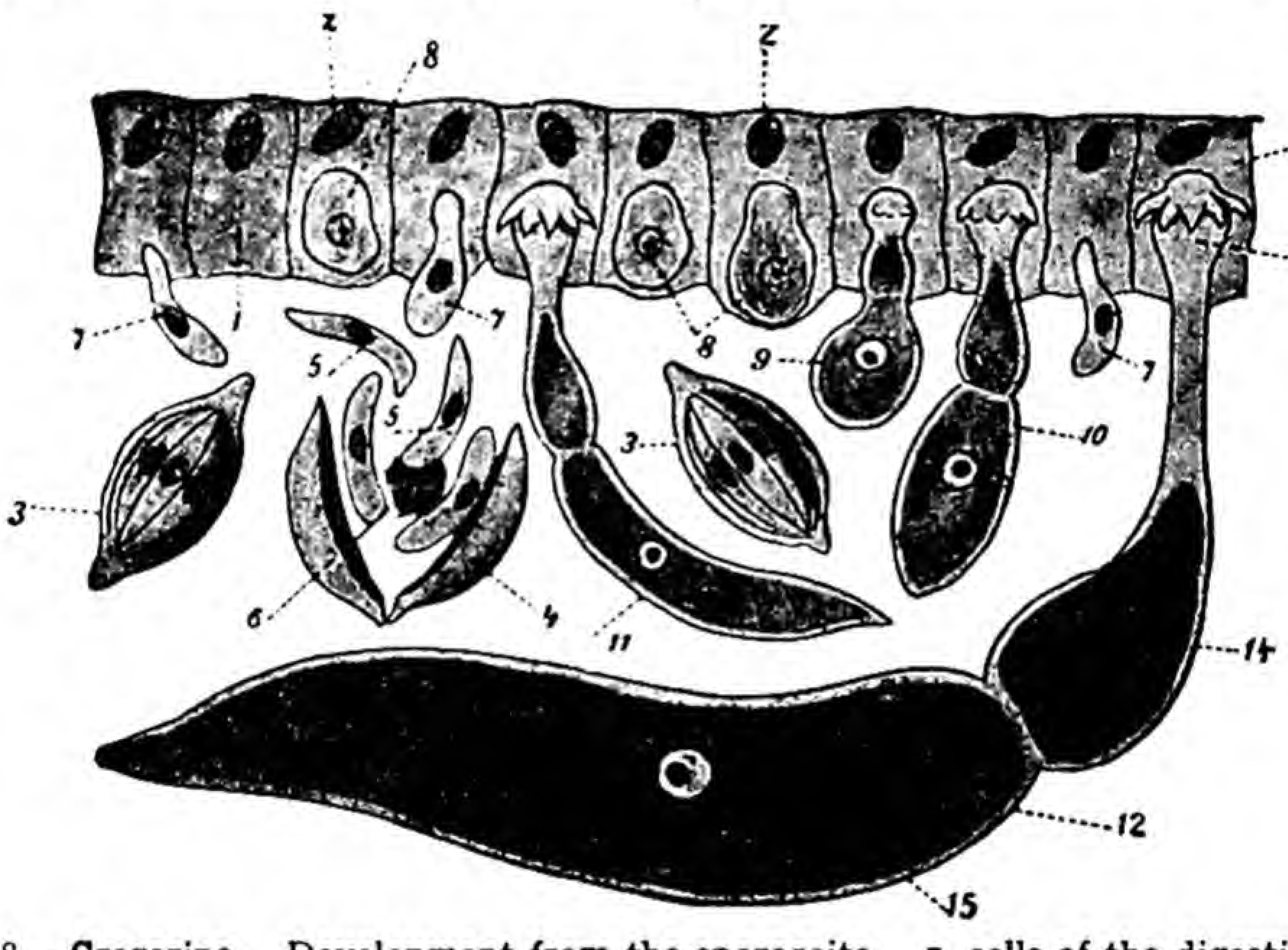


FIG. 68.—**Gregarina.** Development from the sporozoite. *1*, cells of the digestive epithelium of the host; *2*, nuclei of the same; *3*, spore; *4*, spore discharging sporozoites (*5*) leaving residual mass (*6*); *7*, sporozoites in the act of entering epithelial cells; *8*, the same as intracellular parasites; *9–12*, different stages in the growth of the young Gregarines into the lumen of the intestine; *13*, epimerite; *14*, protomerite; *15*, deutomerite. (After Lang.)

epimerite, which may be provided with radiating spine-like projections (Fig. 68). When it escapes from the spore the sporozoite in nearly all cases (Fig. 68, *7*) enters one of the cells of the epithelium of the alimentary canal of some member of the higher animal phyla, and lives and grows there for a time as an intracellular parasite (*8*). As it grows it comes to project into the cavity of the canal (*9*, *10*, *11*, *12*), and may eventually become entirely free therein or in the body-cavity, or remain attached to the cell by the epimerite. The formation of spores in Gregarina and its allies, as in Monocystis, is preceded by the close apposition to one another of two trophozoites and their enclosure in a common cyst. Such conjugating trophozoites in Gregarina, as also in Monocystis, are not of the nature of gametes: they are cells in which gametes are produced

and are appropriately named *gametocytes*. The cells that result from the division of the nuclei and protoplasm of the two associated gametocytes are the true gametes: they copulate, *i.e.*, completely coalesce in pairs, each pair developing into a spore. The two gametes the copulation of which leads to the formation of a spore may be entirely alike; but in some at least of the Gregarinida it is possible to distinguish between two sets of gametes which

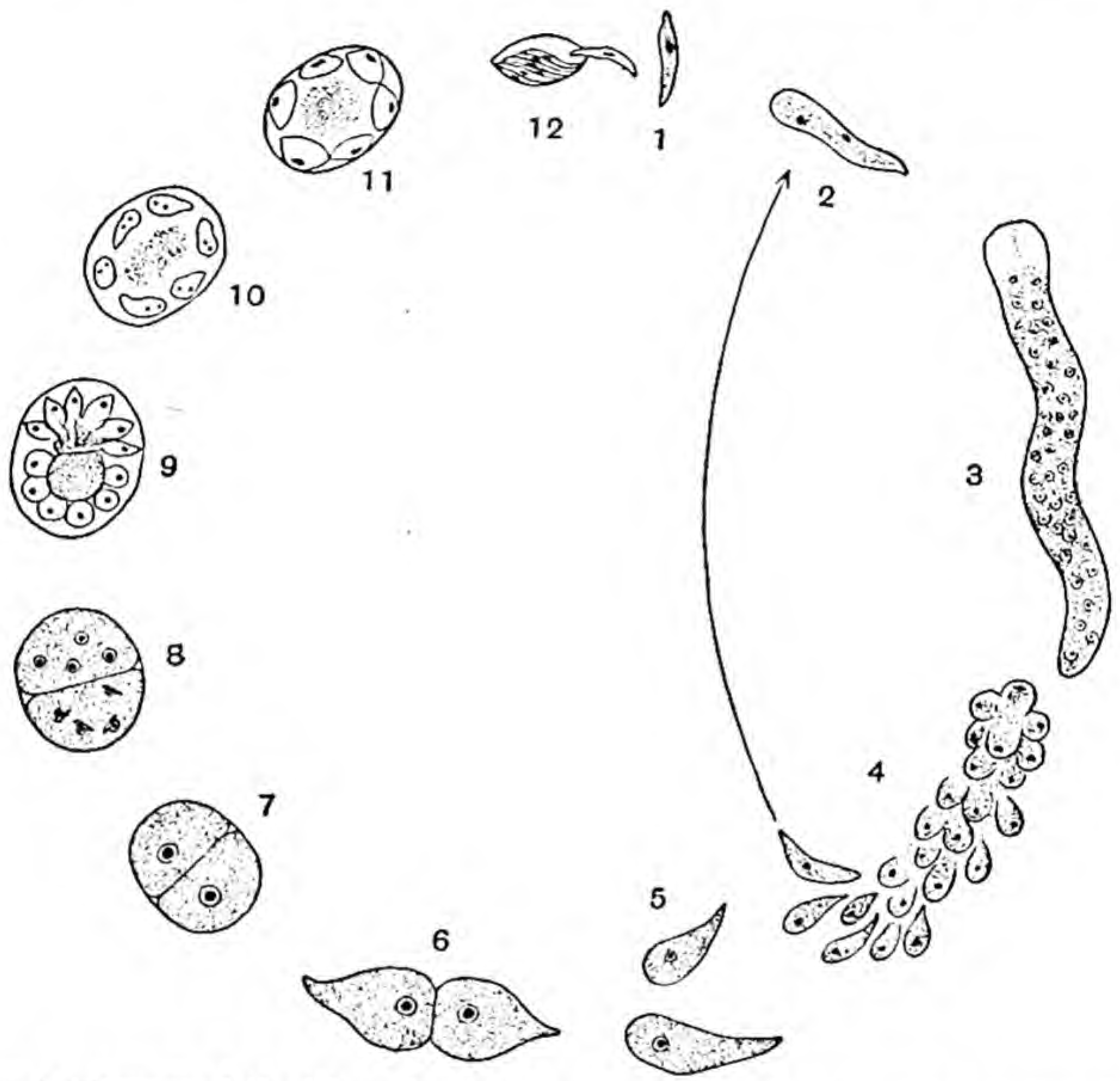


FIG. 69.—A diagram of the life cycle of **Schizocystis.** *1–4*, schizogony; *5*, gametocytes; *6*, syzygy; *7–9*, gamogony in a cyst (gamocyst); *10*, *11*, syngamy; *12*, freed spore case containing sporozoites resulting from sporogony. (After Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge).)

may be looked upon as male and female, copulation taking place between members of the two sets.

In *Schizocystis gregarinoides* (Fig. 69) the sporozoite (*1*) during the period of growth becomes multinuclear (*2*, *3*). When fully grown its body divides into as many so-called merozoites as there are nuclei (*4*). These merozoites may either repeat this process of schizogony (*2*) or grow without becoming multinuclear into an individual (*5*) which associates with a second one to form a common cyst (*6*, *7*) inside which typical spore formation takes place (*8–12*).

ORDER 2.—COCCIDIA.

Eimeria (Fig. 70) and allied genera are parasites in the interior of cells, both in Vertebrates and Invertebrates. They live in the cells of various organs, most frequently in those of the epithelium of the digestive canal. A few are intranuclear parasites. Two distinct modes of multiplication occur—by *schizogony*, a kind of multiple fission, and by *sporogony*, a process of spore-formation preceded by copulation between male and female cells. The *trophozoite*, or adult phase, as we may term it, of the parasite, grows to a certain size within the

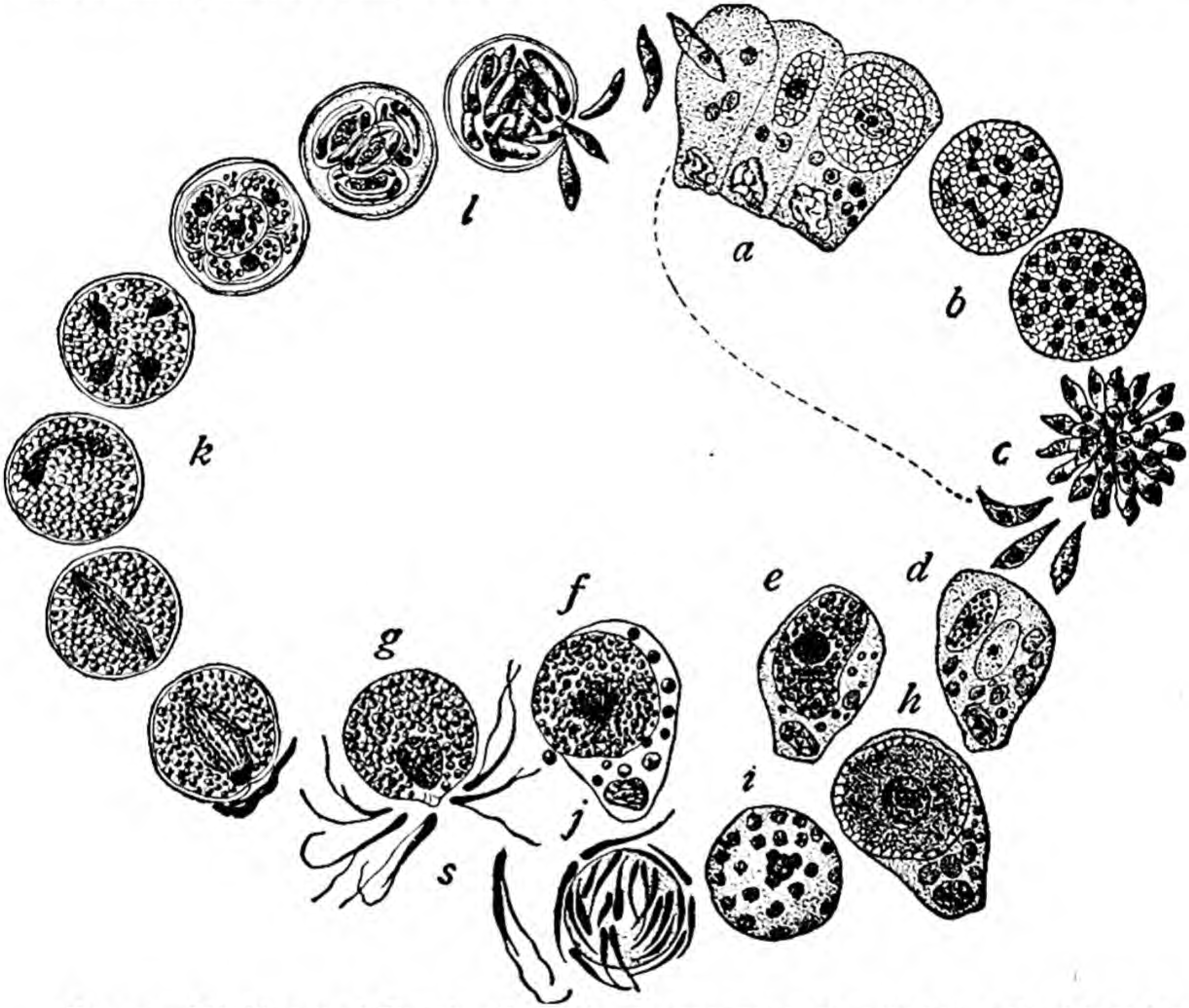


FIG. 70.—Life-history of **Eimeria schubergi.** *a*, penetration of epithelium cell of host by sporozoite; *b–c*, stages of multiple fission (schizogony); *d*, gametocyte; *e*, *f*, formation of macrogamete (ovum); *g*, fertilization; *h*, *j*, formation of microgametes (sperms); *k*, development of fertilized ovum into four spores; *l*, formation of two sporozoites (falciform young) in each spore. (From Calkins, after Schaudinn.)

cell without destroying its vitality—the nucleus merely being pushed on one side. So far, in fact, from impairing the nutrition of the cell, the presence of the parasite seems, in some cases, for a time, rather to stimulate it. At a certain stage of growth schizogony (Fig. 70, *b–c*) takes place. The nucleus divides to form a number of nuclei. These migrate towards the surface, and each becomes surrounded by protoplasm, with the result that a number of small cells are formed. Each of these gives rise to a club-shaped *merozoite*. The merozoites, when they become free, are active bodies, which are able to penetrate into the interior of other epithelial cells and develop into trophozoites like those from which they were derived. This multiplication may take place on such an extensive scale that the

epithelium may be partially or completely destroyed. It is only, apparently, when such extensive damage has been done, or is threatened, that multiplication by sporogony takes place—the invasion of a new host being by this process rendered probable, and the continuance of the race being thus provided for in the event of the death of the host in which the epithelium has become destroyed. In this process certain of the merozoites, instead of developing into trophozoites, grow more slowly (*d*), and become converted into either micro- or macro-gametocytes. Each of the former (*h*, *j*) gives rise by division to a number of narrow biflagellate microgametes or sperms. Each of the macrogametocytes (*e*, *f*), after a process of the nature of maturation, forms a single rounded macrogamete (ovum). When this becomes fertilized by the penetration into it of a single microgamete, the resulting body (*zygote*) divides to form a varying number of cells each enclosed in a resistant cyst (*k*). These give rise to spores with a firm, chitinous spore-membrane, each containing two or more falciform young or *sporozoites* (*l*). The cyst destroys the cell as it grows, and thus becomes free in the cavity by which the epithelium is lined. The spores may thus pass out to the exterior, and, if taken into the digestive canal of a new host, may liberate the now active sporozoites, which may penetrate into epithelial cells (*a*) to become the trophozoites with which the cycle began.

In some of the Coccidia this life-cycle is modified in various ways, as, for example, by the omission of schizogony—the trophozoites in such a case developing directly into gametocytes.

ORDER 3.—HÆMOSPORIDIA.

These are Sporozoa which in the trophozoite condition live as parasites in the interior of the coloured blood-corpuscles of all classes of Vertebrates, but are occasionally found in other cells. In man and in some other mammals and in certain birds it has been found that their presence is the cause of various feverish affections. The various forms of malaria in man have been proved to be due to the presence in the blood-corpuscles of the patient of parasites belonging to this order. The malaria parasites, the history of which has been carefully worked out, pass through a life-cycle comparable to that of *Coccidium* described above. In the trophozoite stage (Fig. 71, *1–5*) they live as amœboid intracellular parasites in the interior of the coloured corpuscles of their host. Here they multiply by schizogony —the products (merozoites, *6*, *7*) entering other corpuscles. Some of the merozoites when they become established in the interior of the corpuscles develop into rounded or crescentic bodies which become the gametocytes (*8*, *9*). In order that the life-cycle may be completed, it is necessary that the parasite at this stage should be taken into the interior of a second or intermediate host. In the case of the parasite of human malaria the intermediate host is a mosquito of the genus *Anopheles*. On the mosquito drawing up a drop of the blood of a malaria patient, all stages of the parasite that occur in it are destroyed by the digestive juices of the insect, with the exception of the gametocytes; these survive and form gametes in the stomach of the mosquito. Each male gametocyte gives rise to a number of slender filamentous microgametes (sperms, *10a*, *11a*) and each female gametocyte forms a single macrogamete (ovum, *10b*, *11b*). After maturation the macrogamete is fertilized (*12*) by one of the actively moving microgametes, the result being the formation of an active spindle-shaped zygote called *ookinete* or *vermicule* (*13*). This perforates the stomach-wall and comes to rest in the subjacent tissues. It then becomes encysted and increases greatly in size, bulging out into the body-cavity (*14*, *15*). The contents of the cyst eventually divide up (*16–18*) into a large number of long, narrow sporozoites. When the cyst becomes ruptured into the body-cavity, these find their way to the salivary glands (*19*), and thence they may readily be transferred to the blood-system of a human being when the mosquito bites. Penetrating into the interior of coloured corpuscles they reach the trophozoite condition.

Malaria in Man is caused by three species of malaria parasites: *Plasmodium vivax*, *Plasmodium malariæ*, and *Plasmodium falciparum*. The morphological differences between these three species are small, but they differ characteristically in the time interval required for a complete schizogonous cycle. Thus in *Plasmodium vivax* a new generation of merozoites is liberated into the blood-stream every forty-eight hours, in *Plasmodium malariæ* every seventy-two hours, and in *Plasmodium falciparum* at irregular intervals. Since the attacks of fever are caused by toxic substances which are set free when the blood-corpuscles break up, the malaria-attacks caused by *Plasmodium vivax* recur every third day (*Tertian ague*) those caused by *Plasmodium malariæ* every fourth day (*Quartan ague*). The

pernicious malaria of the tropics caused by *Plasmodium falciparum*, owing to its irregular rhythm, is characterized by almost continuous fever.

The *Hæmogregarines*, which may most conveniently be referred to here, are Sporozoa which live in the coloured blood-corpuscles of all classes of Vertebrates, but chiefly in

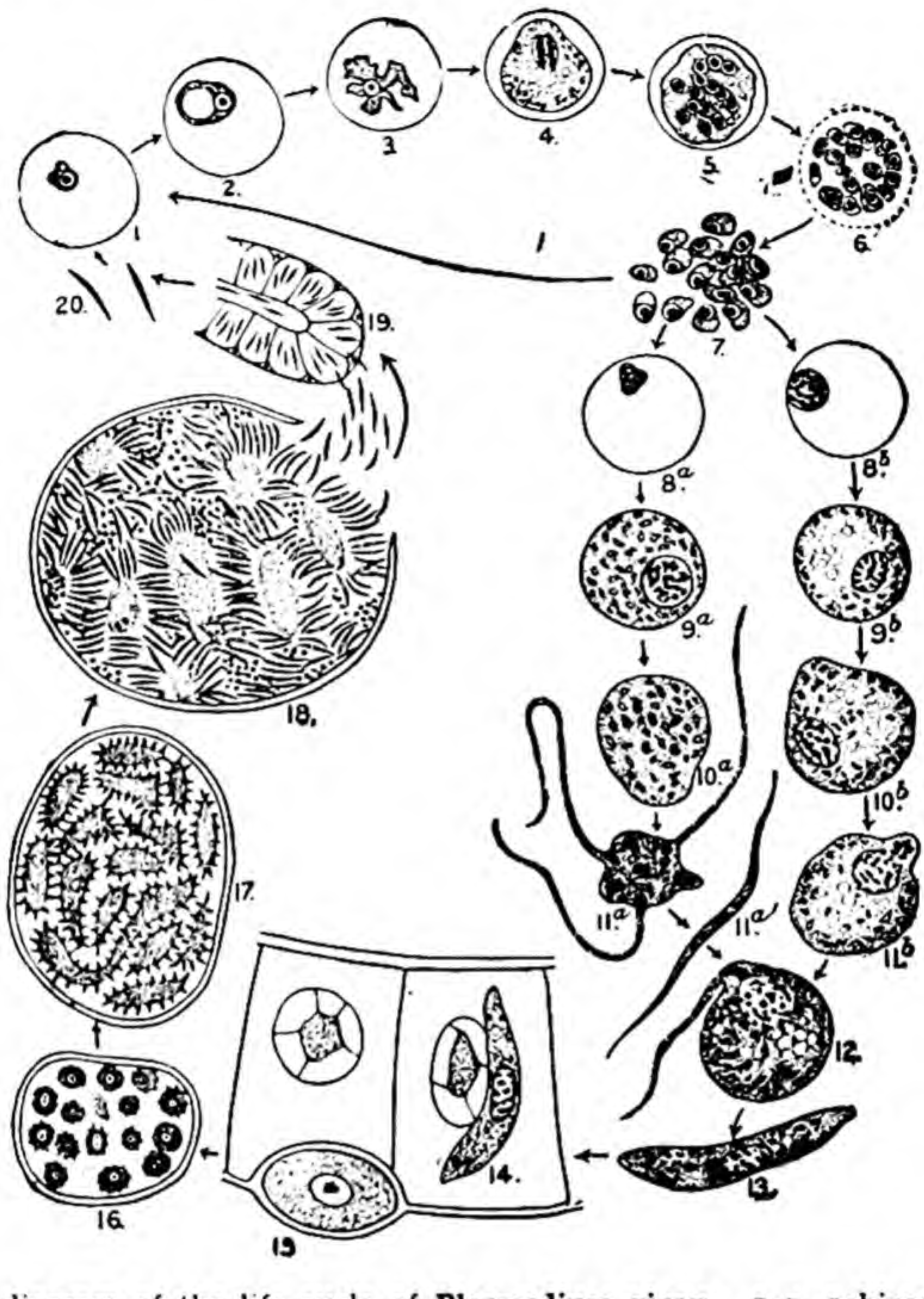


FIG. 71.—A diagram of the life cycle of **Plasmodium vivax.** *1–7*, schizogony (merogony), asexual reproduction which takes place in Man. *8–13*, gamogony and syngamy, which take place in the stomach of a mosquito. *14–20*, sporogony by the zygote (sporont), which takes place in the body cavity of the mosquito; *1*, infection of a red corpuscle; *2*, signet ring stage; *3*, amœboid stage; *4*, full-grown schizont preparing to divide; *5*, multinucleate stage; *6*, rosette stage, corpuscle breaking up; *7*, free merozoites; *8*, infection of red corpuscles by young gametocytes; *9*, full-grown gametocytes free in the mosquito's stomach; *10*, *11*, formation of gametes; *12*, conjugation; *13*, zygote in the ookinete condition; *14*, invasion by zygote of endoderm cell of mosquito; *15*, encystment; *16*, sporoblasts formed by division of zygote (sporont); *17*, *18*, formation of sporozoites; *19*, invasion by latter of salivary gland; *20*, sporozoites injected into blood of Man. (After Borradaile's *Manual of Elementary Zoology* (Oxford University Press).)

Fishes, Amphibians, and Reptiles; but which, unlike the malaria parasites, in the mature or trophozoite condition are not amœboid, retaining the Gregarina-like form and undergoing syzygy. Transference from one host to another is effected by means of various blood-sucking Invertebrates. The Hæmogregarines are now frequently included among the Coccidia.

Sub-class II.—Neosporidia.

ORDER 1.—MYXOSPORIDIA.

This group includes a number of genera which are amœboid in the trophozoite phase, and which reproduce continuously by spore-formation during that phase (Fig. 72, *A*). Many nuclei are present in the amœboid body, which may be of comparatively large size. The spores (*B*) produced within the protoplasm of the trophozoite are provided each with

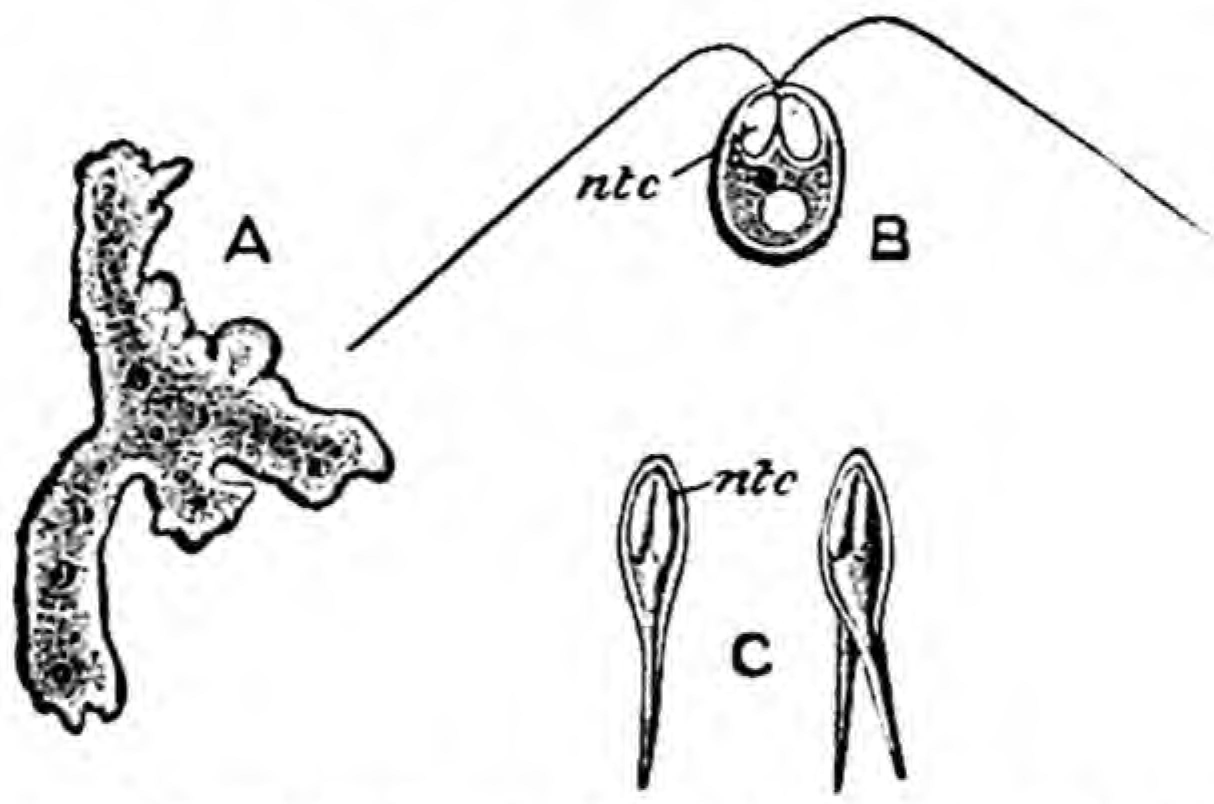


FIG. 72.—*A*, **Myxidium lieberkühnii,** amœboid phase; *B*, **Myxobolus mülleri,** spore with discharged nematocysts (*ntc.*); *C*, spores of a Myxosporidian; *ntc.* nematocysts. (From Bütschli's *Protozoa.*)

one or more bodies like the nematocysts of Cœlenterates [See Section IV]. Myxosporidia occur as parasites mainly of Fishes and Amphibians, but very many occur in various groups of Invertebrates. "Pébrine," the destructive silk-worm disease, is due to the presence of Nosema. A good example of the order is *Myxidium*, found in the urinary bladder of the Pike.

ORDER 2.—SAROCOSPORIDIA.

The best-known form of this order is *Sarcocystis* (Fig. 73), which occurs in the flesh of Mammals, each parasite having the form of a long spindle embedded in a striped

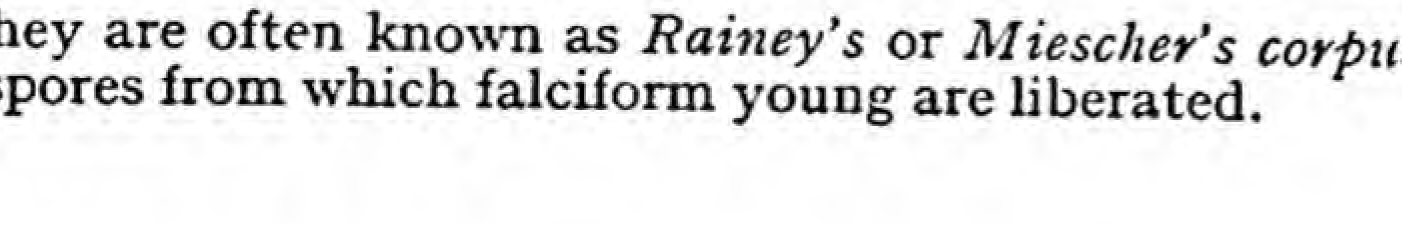


FIG. 73.—**Sarcocystis miescheri,** adult form (*s*) in striped muscle of pig. (From Bütschli's *Protozoa*, after Rainey.)

muscular fibre. They are often known as *Rainey's* or *Miescher's corpuscles.* The protoplasm divides into spores from which falciform young are liberated.

CLASS V.—CILIOPHORA.

1. EXAMPLE OF THE CLASS—*Paramecium caudatum.*

Structure.—*Paramecium*, the "slipper-animalcule," is common in stagnant ponds, organic infusions, etc. The body (Fig. 74) is about $\frac{1}{4}$ mm. in length,

somewhat cylindrical, but flattened, with distinct upper and lower or dorsal and ventral surfaces, and anterior and posterior ends, the latter rather more pointed than the former. On the ventral face is a large oblique depression, the *peri-*

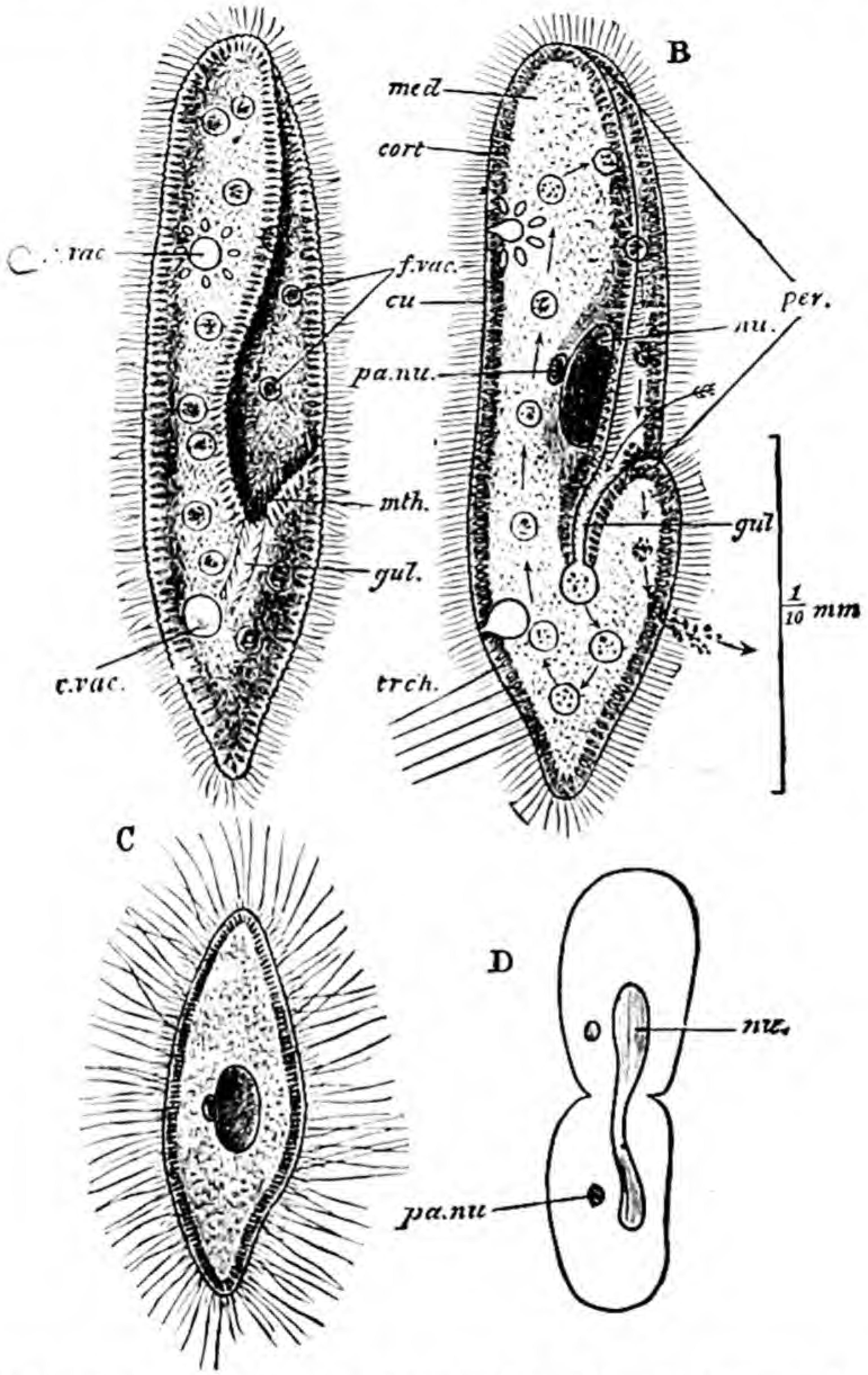


FIG. 74.—**Paramecium caudatum.** *A*, the living animal from the ventral aspect; *B*, the same in optical section: the arrow shows the course taken by food-particles; *C*, a specimen which has discharged its trichocysts; *D* diagram of binary fission; *cort.* cortex; *cu.* cuticle; *c. vac.* contractile vacuole; *f. vac.* food vacuole; *gul.* gullet; *med.* medulla; *nu.* macronucleus; *pa. nu.* micronucleus; *per.* peristome; *trch.* trichocysts. (From Parker's *Biology*.)

stome (*per.*), leading into a short *gullet* (*gul.*), which, as in Euglena, ends in the soft internal protoplasm.

The body is covered with small cilia arranged in longitudinal rows and continued down the gullet. The protoplasm is very clearly differentiated

into a comparatively dense *cortex* (*cort.*) and a semi-fluid *medulla* (*med.*), and is covered externally by a thin *pellicle* or *cuticle* (*cu.*) which is continued down the gullet. Each of the cilia is connected at its base with a very small basal granule (rendered visible only by special staining of fixed specimens) situated below the pellicle.

In more or less close contact with the cortex are found two nuclei, the relations of which are very characteristic. One, distinguished as the *macronucleus* (*nu.*), is a large ovoid body which, when it divides, does so directly by a simple process of constriction. The other, called the *micronucleus* (*pa. nu.*), is a very small body closely applied to the macronucleus; when it divides it goes through the complex series of stages characteristic of mitosis.

The contractile vacuoles (*c. vac.*) are two in number, and are very readily made out. Each is connected with a series of radiating spindle-shaped cavities in the protoplasm which serve as feeders to it. After the contraction of the vacuole these cavities are seen gradually to fill, apparently receiving water from the surrounding protoplasm: they then contract, discharging the water into the vacuole, the latter rapidly enlarging while they disappear from view; finally the vacuole contracts and discharges its contents externally.

The cortex contains minute radially arranged spindle-shaped bodies called *trichocysts* (*trch.*). When the animal is irritated more or fewer of these suddenly discharge a long delicate thread. In a specimen killed with iodine or osmic acid the threads can frequently be seen projecting in all directions from the surface (*C*).

Food, in the form of small living organisms, is taken in by means of the current caused by the cilia of the peristome. The food-particles, enclosed in a globule of fluid or " food-vacuole " (*f. vac.*), circulate through the protoplasm, when the soluble parts are gradually digested and assimilated. Effete matters are egested at a definite *anal spot* posterior to the mouth, where the cortex and cuticle are less resistant than elsewhere. The whole feeding process can readily be observed in this and other Ciliophora by placing in the water some insoluble colouring matter, such as carmine or lamp-black, in a fine state of division.

Reproduction.—Multiplication takes place by transverse binary fission (*D*), the division of the body being preceded by that of both nuclei. As already mentioned, the macronucleus divides by simple constriction, the micronucleus mitotically. Fission is never associated with encystation as it is in *Euglena*.

Under certain conditions multiplication by fission is interrupted by *conjugation*. In this very remarkable and characteristic process two Paramecia become applied by their ventral surfaces (Fig. 75, I), but do not fuse. The macronucleus (*ma.*) of each breaks up into small masses, which eventually disappear, being apparently absorbed into the protoplasm. At the same time the micronucleus (*mi.*) of each divides, each product of division immedi-

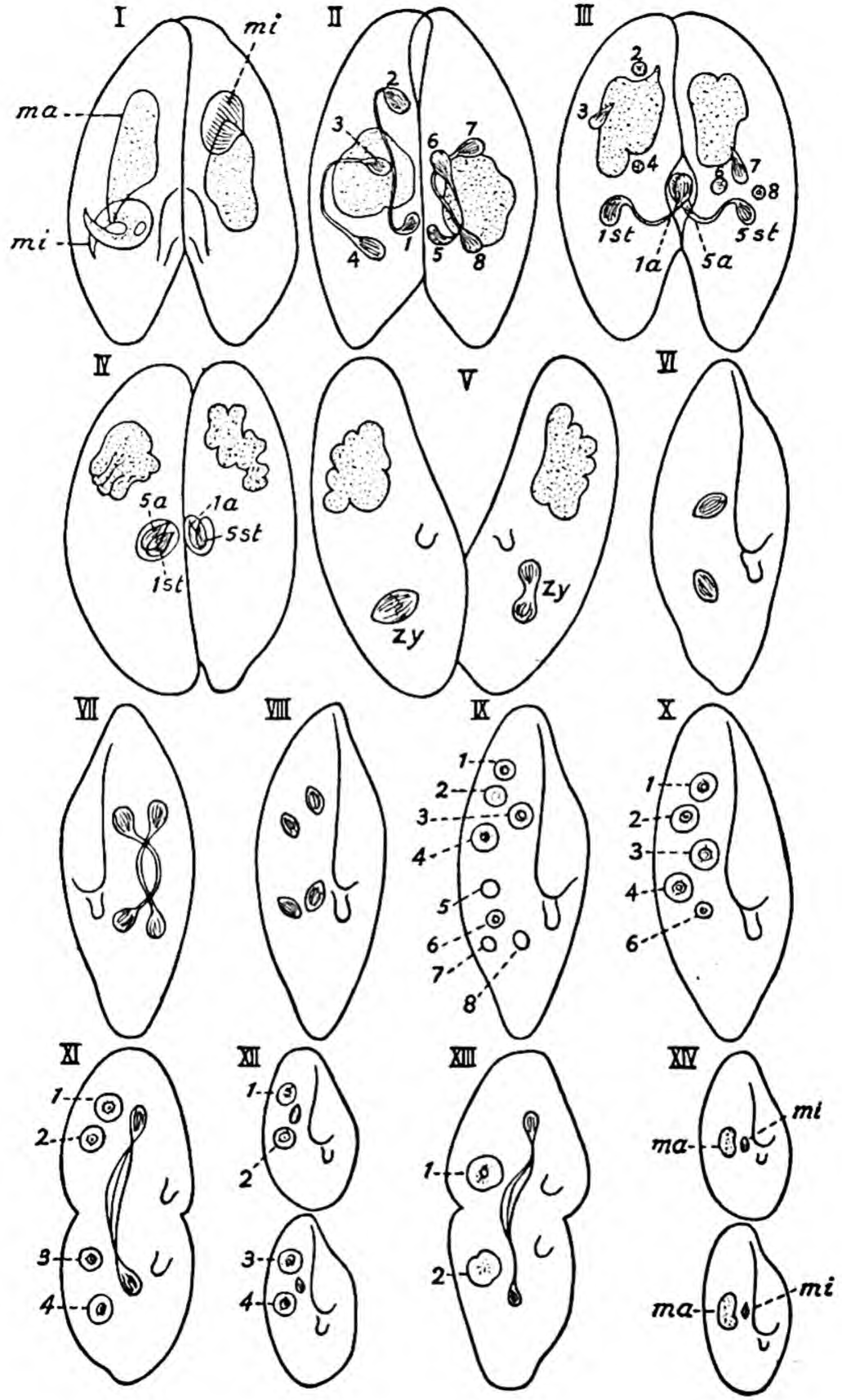

I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
ma
mi
1st
5st
1a
5a
zy

FIG. 75.—**Paramecium caudatum,** stages in conjugation. I–IV, process of conjugation; V–XIV, processes of nuclear reconstruction; I, beginning of mitosis of micronucleus; II, second division of micronucleus in progress; III, stationary pronucleus (*1st, 5st*); active pronucleus (*1a, 5a*) passing into fellow conjugant; *2, 3, 4,* and *6, 7, 8,* abortive micronuclei; IV, fusion of stationary and active pronuclei; V, first division of zygote-nucleus (*zy.*); separation of conjugants; VI, exconjugant with two daughter nuclei; VII, VIII, exconjugants with four daughter nuclei; IX, exconjugant with eight daughter nuclei, four prospective macronuclei (*1–4*), one prospective micronucleus (*6*) and three abortive micronuclei (*5, 7, 8*); X, exconjugant after disappearance of abortive micronuclei; XI, XII, first transverse fission; XIII, XIV, second transverse fission resulting in daughter individuals with normal nuclear arrangement; *ma.* macronucleus; *mi.* micronucleus; *zy.* zygote-nucleus. (From Doflein-Reichenow's *Lehrbuch der Protozoenkunde* (Gustav Fischer, Jena), after various authors.)

ately dividing again, so that each conjugating body is provided with four micronuclei (II). Three of these (III, *2–4*; *6–8*) disappear; the fourth divides again into two, of which one is distinguished as the *stationary pronucleus*, the other as the *active pronucleus*. The active pronucleus of each conjugant now passes into the body of the other and fuses with its stationary pronucleus (III and IV), each individual thus coming to possess a single nuclear body derived in equal proportions from the two conjugating cells. The animalcules then separate from one another, and the nucleus of each divides and gives rise to the permanent macro- and micronuclei (V–XIV), the original nuclear condition becoming completely established only after the two animals have separated and have undergone three mitotic nuclear divisions followed by two transverse fissions.

2. Classification and General Organization.

In the majority of the Ciliophora the body is ciliated throughout life, but in certain forms cilia are present only in the immature condition, the adult being provided with peculiar organs of prehension or *tentacles*. We thus get the following sub-classes and orders:

Sub-class I.—Ciliata.

Ciliophora provided with cilia throughout life.

Order 1.—Holotricha.

Ciliata with small, nearly equal-sized cilia arranged in longitudinal rows; sometimes with gullet and undulating membrane.

Examples: *Opalina* (Fig. 80), *Paramecium* (Fig. 74), and others (Fig. 76, *1, 5, 8, 11, 15, 17, 18, 19*).

Order 2.—Heterotricha.

Ciliata possessing gullet with undulating membrane; peristome with clockwise spiral of large oral cilia; small cilia covering the rest of the body.

Examples: *Nyctotherus* (Fig. 76, *2*), *Stentor* (Fig. 76, *3*), and others (Fig. 76, *4, 6, 10, 16*; Fig. 77, *1*).

Order 3.—Hypotricha.

Dorso-ventrally flattened Ciliata possessing ventral gullet with undulating membranes; oral spiral of cilia curving clockwise; cilia almost confined to ventral side forming a system of locomotory cirri.

Examples: *Diophrys* (Fig. 76, *7*), *Stylonychia* (Fig. 76, *13*), *Stichotricha* (Fig. 77, *5*).

Order 4.—Peritricha.

Mostly sessile Ciliata possessing gullet with undulating membrane; oral spiral of cilia curving anticlockwise; rest of body generally without cilia.

Examples: *Epistylis* (Fig. 76, *9*), *Vorticella* (Fig. 78), *Zoothamnium* (Fig. 79), and others (Fig. 77, *2–4*).

Sub-class II.—Suctoria.

Ciliophora possessing cilia in the young condition, tentacles in the adult.

Examples: *Acineta* and others (Fig. 81).

Sub-class I.—Ciliata.

This sub-class and its orders present a wider range of variations—some of them of a truly extraordinary character—than any other group of Protozoa.

The **form of the body** is very varied: it may be ovoid (Fig. 76 *1*), kidney-shaped (*2*), trumpet-shaped (*3*), vase- or cup-shaped (*4*, *9*); produced into a long, flexible, neck-like process (*5*), or into large paired lappets (*6*); flattened from above downwards, or elongated and divided into segments reminding us of those of a segmented worm (*8*).

Most species are free-swimming, but some are attached to weeds, stones, etc., by a **stalk**. This may be a purely cuticular structure (*9*), or may contain a prolongation of the cortex in the form of a delicate contractile *axial fibre* (Figs. 78 and 79, *ax. f.*), which serves to retract the animal, its contraction causing the stalk to coil up into a close spiral.

The **arrangement of the cilia** on which is based the subdivision of the sub-class into orders, is also subject to great variation, and presents four chief types. In the *holotrichous type*, of which Paramecium is an example, the cilia are all small, equal-sized or nearly so, and arranged in longitudinal rows (Fig. 74, Fig. 76, *1*). The second or *heterotrichous* type is seen in its simplest form in *Nyctotherus* (Fig. 76, *2*), in which the left side of the peristome is bordered by a row of specially large *adoral* cilia, the rest of the body being covered with small cilia. In *Stentor* (*3*) the peristome is situated on the broad distal end of the trumpet-shaped body, and the adoral band of cilia takes a spiral course. This leads us to the *peritrichous* type of ciliation: in *Vorticella* (Fig. 78) the

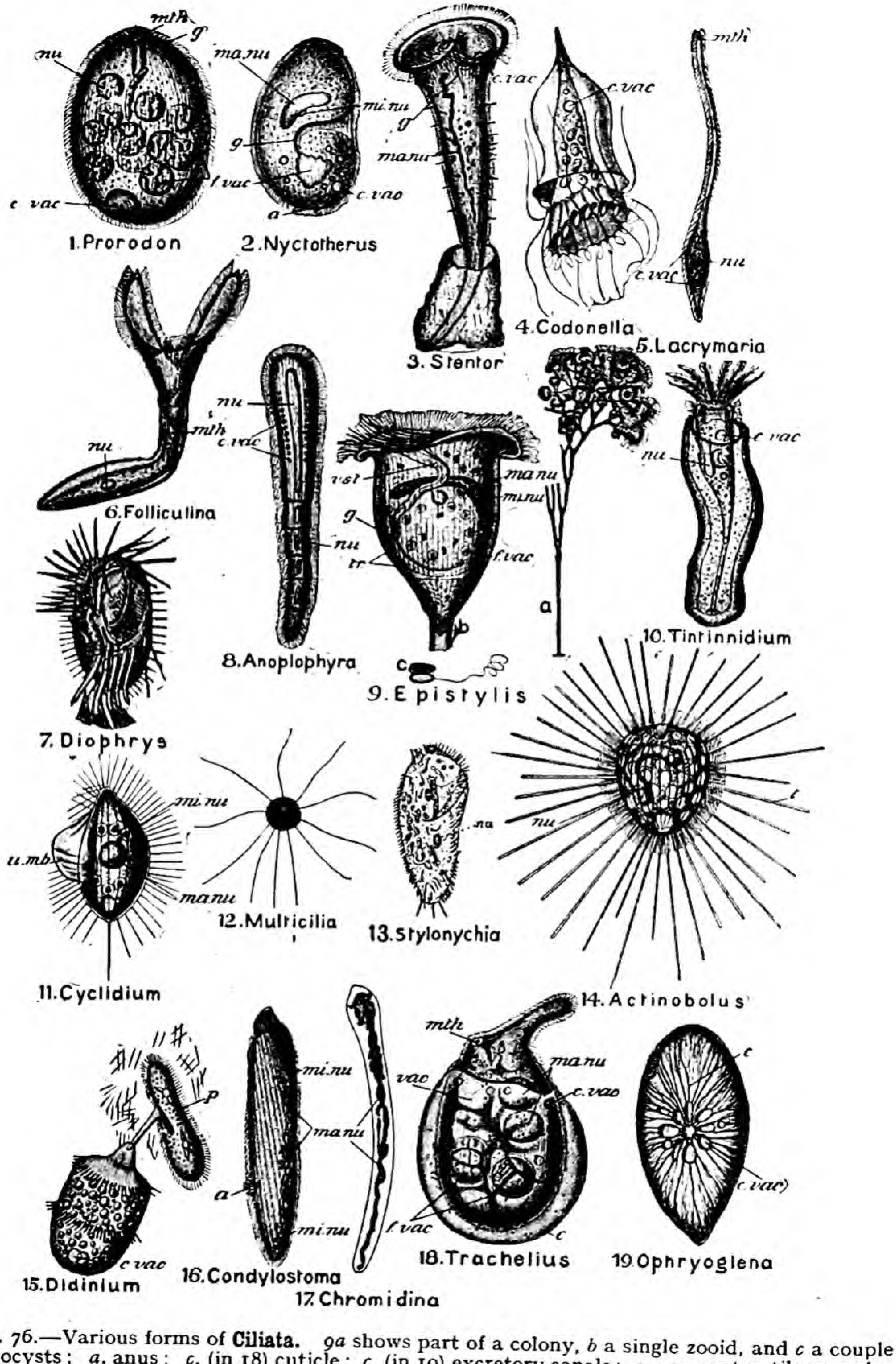


FIG. 76.—Various forms of **Ciliata.** *9a* shows part of a colony, *b* a single zooid, and *c* a couple of trichocysts; *a.* anus; *c.* (in 18) cuticle; *c.* (in 19) excretory canals; *c. vac.* contractile vacuole; *f. vac.* food vacuole; *g.* gullet; *ma.nu.* macronucleus; *mi.nu.* micronucleus; *mth.* mouth; *nu.* nucleus; *p.* (in 15) a *Paramecium* seized by *Didinium*; *t.* tentacle; *tr.* trichocyst; *u. mb.* undulating membrane; *vac.* non-contractile vacuole; *vst.* vestibule. (From Bütschli's *Protozoa*, after various authors.)

vase-shaped body is, for the most part, quite bare of cilia, but around the thickened edge of the peristome passes one limb of a spiral band of large cilia united at their bases, the other limb being continued round a raised lid-like structure, or *disc*, into which the distal region is produced. This arrangement of cilia reaches its greatest complexity in *Epistylis plicatilis* (Fig. 76, *9*), in which the ciliary spiral makes no fewer than four turns. But it is in the *hypotrichous* type that the most extraordinary modifications are found. The flattened body bears on its dorsal surface mere vestiges of cilia in the form of very minute processes, while on the ventral surface the cilia take the form of large hooks, fans, cirri, and plates with fringed ends (Fig. 76, *7*, *13*). The hooks and plates do not vibrate rhythmically like ordinary cilia, but are moved as a whole, thus acting as legs. The hypotrichous Ciliata, in fact, in addition to swimming freely in the water, creep over the surface of weeds, etc., very much after the manner of Woodlice. One of the most extraordinary forms in this group is *Diophrys* (*7*), the size and arrangement of its polymorphic cilia giving it a very grotesque appearance.

In addition to cilia, many genera possess delicate sheets of protoplasm or *undulating membranes* in connection with the peristome. They contract so as to produce a wave-like movement which aids in the ingestion of food. In some cases (Fig. 76, *11*) the undulating membrane (*u. mb.*) is a very large and obvious structure.

Certain peculiar forms have yet to be mentioned. *Multicilia* (Fig. 76, *12*), which is now considered to be more closely related to the Mastigophora, has an irregular body of varying form, and bears a small number of very long flagellum-like cilia. *Actinobolus* (*14*) is remarkable for the possession, in addition to cilia, of long retractile tentacles used for attachment. In *Didinium* (*15*) the barrel-shaped body is encircled by two hoops of cilia.

As we have seen, the **macronucleus** in *Paramecium* is ovoid : in other genera it may be elongated and band-like (*3*, *ma. nu.*), horseshoe-shaped (*9*), very long and constricted at intervals so as to look like a string of beads (*16*), or much convoluted and branched (*17*). In some genera the macronucleus undergoes repeated division, forming at last a very great number of small bodies (*chromidia*) only discoverable by staining : this process of *fragmentation of the nucleus* may proceed so far that the protoplasm of a stained specimen has the appearance of being strewn with granules of chromatin. The discovery of this phenomenon has tended to throw doubt on the reported total absence of a nucleus in some Rhizopods.

In nearly all species one or more **micronuclei** are present, the number sometimes reaching nearly thirty. In *Opalina* (Fig. 80) numerous nuclear bodies (*nu.*) are present, some of which on account of their mitotic mode of division are to be regarded as micronuclei, while the rest are macronuclei.

In *Vorticella* and other peritrichous genera, there is a single **contractile**

vacuole (Fig. 78, *c. vac.*), which, like that of Euglena, opens through the intermediation of a reservoir into the vestibule. In the remaining Ciliata there may be one, two, or many—sometimes a hundred—contractile vacuoles. They may be scattered all over the cortex (Fig. 76, *18*), or arranged in one or two rows (*8*). The star-like arrangement of radiating canals, described in Paramecium, occurs in several genera: or there may be two long canals, or the number of these channels in the protoplasm may reach thirty (*19, c*). In some instances the protoplasm is hollowed out by numerous **non-contractile vacuoles** (*18, vac.*) so as to have a reticulate appearance, reminding us of the extra-capsular protoplasm of Radiolaria.

Trichocysts, like those of Paramecium, are found in many holotrichous forms, but are rarely present in the other orders. In the peritrichous

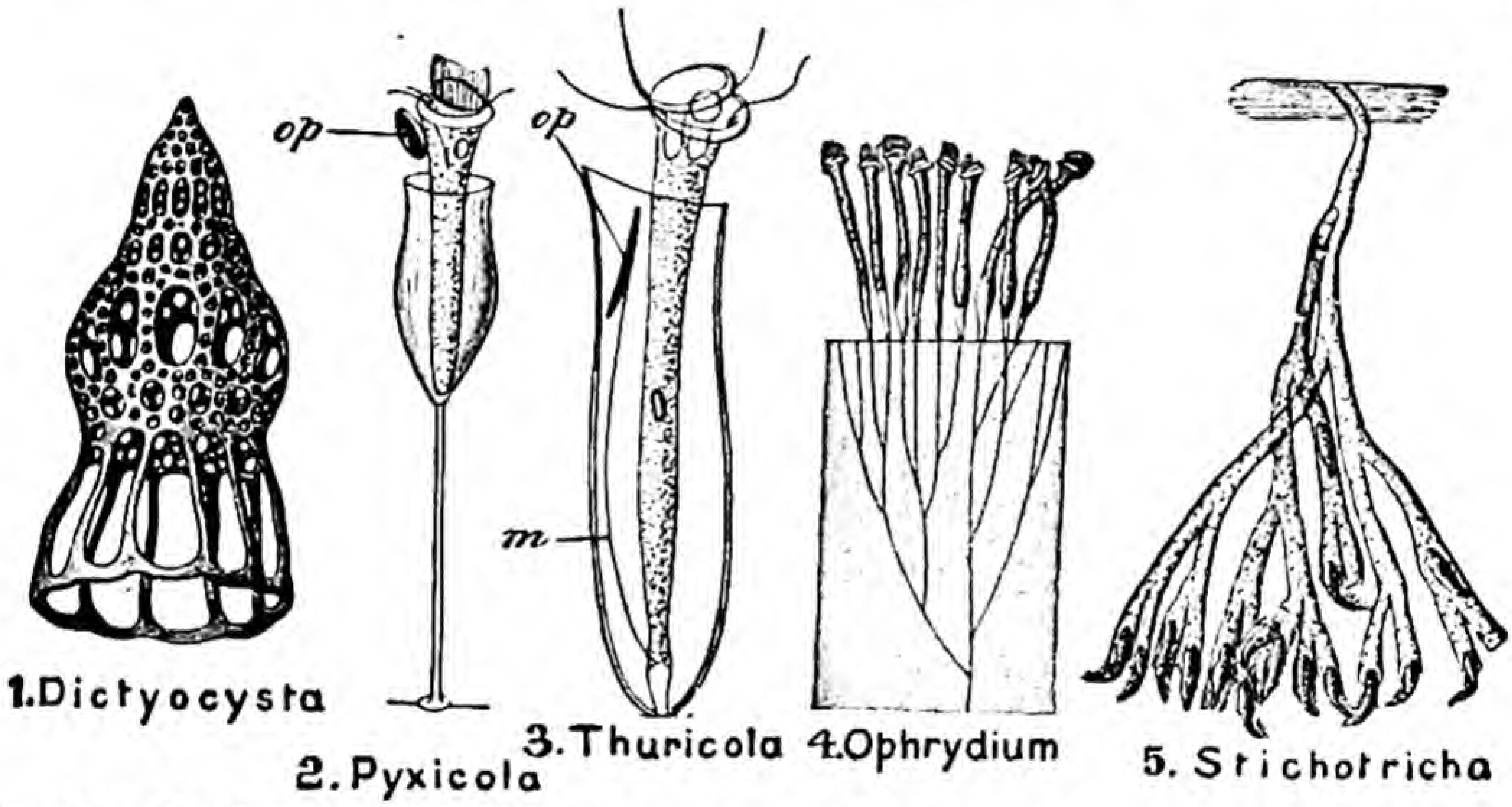


FIG. 77.—Various forms of **Ciliata.** In *1* the shell alone is shown; *m.* contractile fibre; *op.* operculum. (From Bütschli's *Protozoa*, after various authors.)

Epistylis umbellaria, however, there are found numerous minute capsules (Fig. 76, *9, tr.*) arranged in pairs, each containing a coiled thread. They are obviously structures of the same character as trichocysts, and their resemblance to the *nematocysts* so characteristic of Cœlenterata (*vide* Section IV) is singularly close.

Digestive Apparatus.—Many parasitic forms (Fig. 76, *8, 17*; Fig. 80) have no mouth or gullet, and are nourished by absorption of the digested food in the intestine of their host. The simplest condition of the ingestive apparatus is found in *Prorodon* (Fig. 76, *1*) and its allies, in which the mouth (*mth.*) is at one pole of the ovoid body, and is closed except during the ingestion of food, and the gullet (*g.*) is a short, straight tube. Such forms, on account of the symmetrical disposition of their organs and the want of differentiation of their cilia—they are all holotrichous—may be considered as the lowest or least

specialized of the Ciliata. From them there is a fairly complete gradation to genera, like Paramecium, having the permanently open mouth on the left side of the ventral surface, at the end of a well-marked peristome. *Vorticella* (Fig. 78) and its allies are peculiar in having the edge of the peristome (*per.*) thickened so as to form a projecting rim, and in the development of an elevated disc (*d.*) from the area thus enclosed: the mouth (*mth.*) lies between the peri-

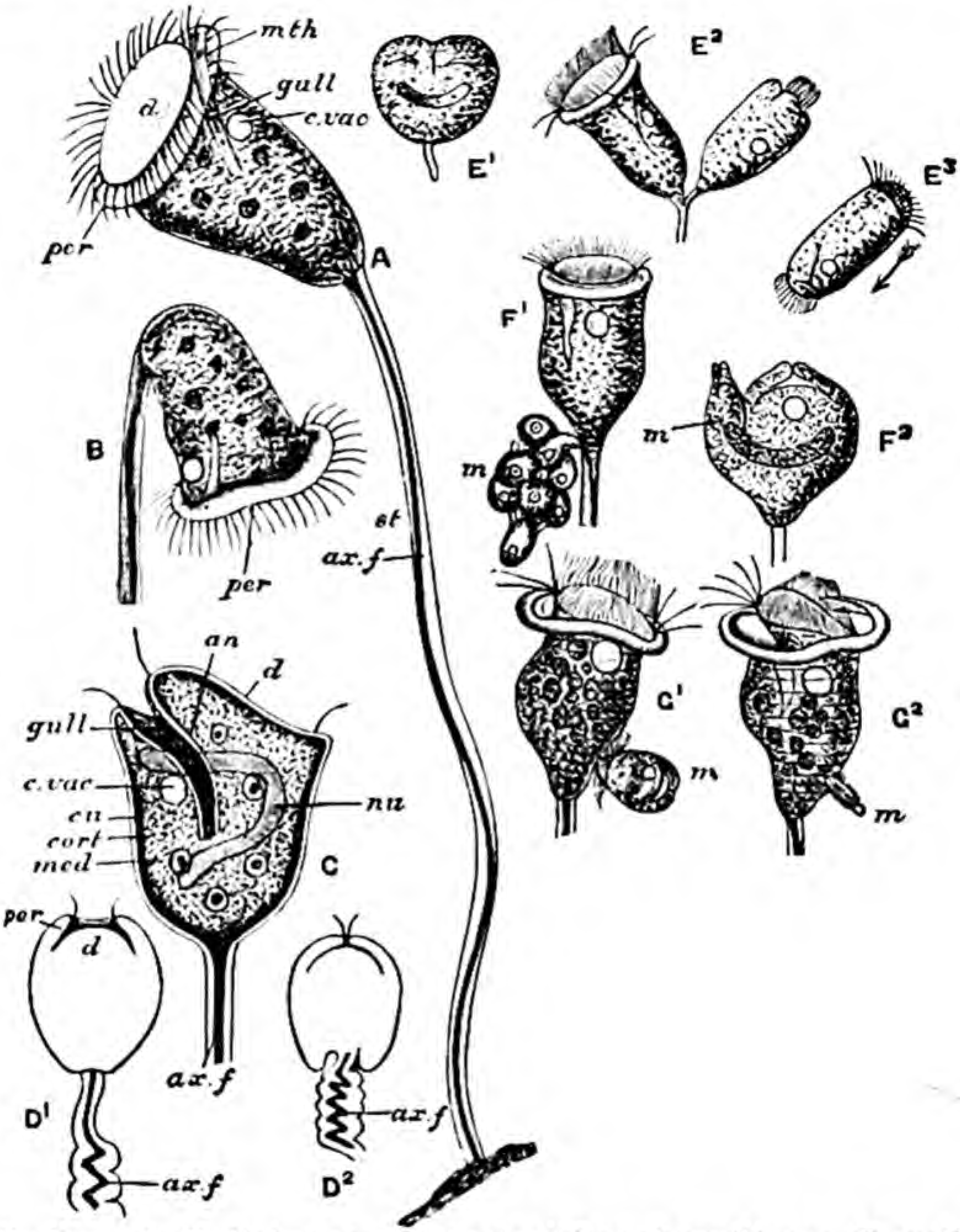


FIG. 78.—**Vorticella.** *A, B,* living specimens in different positions; *C,* optical section; D^1, D^2, diagrams illustrating coiling of stalk; E^1, E^2, two stages in binary fission; E^3, free zooid; F^1, F^2, two modes of division into macro- and micro-zooids; G^1, G^2, conjugation; *ax. f.* axial fibre; *cort.* cortex; *cu.* cuticle; *c. vac.* contractile vacuole; *d.* disc; *gull.* gullet; *m.* microzooid; *mth.* mouth; *nu.* macronucleus; *per.* peristome. (From Parker's *Biology*.)

stome and the disc, and between it and the gullet proper (*gull.*) is interposed a section of the ingestive tube called the *vestibule* into which the reservoir opens, and which contains the anal spot. In *Nyctotherus* (Fig. 76, 2) and some other genera there is, instead of the temporary anal spot described in Paramecium, a distinct *anal aperture* (*a.*).

Most of the Ciliata are naked, having no shell or other form of **skeleton;** but in a few forms the body is provided with a shell or *lorica*, formed of a

chitinoid material, and reminding us of the similar structure found in so many of the Mastigophora. Some (Fig. 76, *4*) have bell-like shells, variously ornamented, and in others (Fig. 77, *1*) the similarly shaped shell is perforated and resembles the skeleton of some of the Radiolaria. A chitinoid plate or *operculum* (Fig. 77, *2*, *op.*) may be fixed to the edge of the peristome, and, when the animal is retracted in its case, accurately closes the mouth of the latter, or a similar operculum (*3*) is attached to the interior of the tube, and is closed by a contractile thread of protoplasm (*m.*), which acts as a retractor muscle.

Compound forms or **colonies** are common among the Peritricha, rare in the other orders. Many peritrichous forms occur as branched, tree-like colonies, often of great complexity (Fig. 76, *9a*; Fig. 79). The stem of these may be a purely cuticular structure and non-contractile (Fig. 76, *9b*,) or may

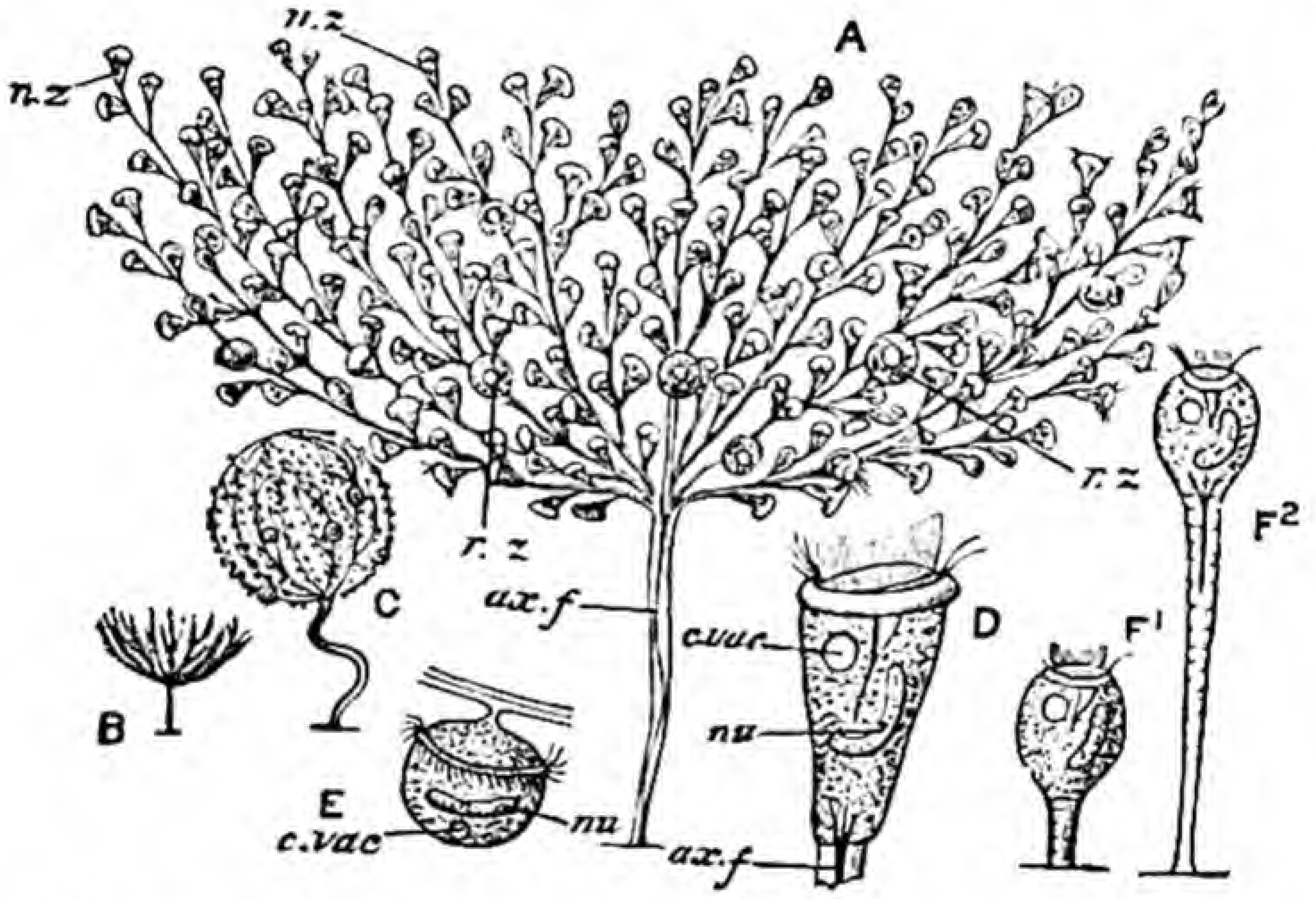


FIG. 79.—**Zoothamnium arbuscula.** *A*, entire colony; *B*, the same, natural size; *C*, the same, retracted; *D*, nutritive zooid; *E*, reproductive zooid; *F*¹, *F*², development of reproductive zooid; *ax. f.* axial fibre; *c. vac.* contractile vacuole; *nu.* nucleus; *n. z.* nutritive zooid; *r. z.* reproductive zooid. (From Parker's *Biology*, after Saville Kent.)

contain an axial fibre or muscle, like that of Vorticella (Fig. 78, *ax. f.*). In *Ophrydium* (Fig. 77, *4*) the colony is an irregular mass, sometimes 4–5 in. in diameter, consisting of a gelatinous substance in which a delicate, branching stem is embedded, each branch terminating in a zooid. Some genera (Fig. 77, *5*) secrete a hollow, brown, gelatinous tube, branched dichotomously; the end of each branch is the habitation of one of the zooids.

Reproduction.—*Transverse fission* is the universal method of reproduction, the entire process taking from half an hour to two hours in different species. In Vorticella (Fig. 78, *E*) and other Peritricha the plane of division is parallel to the long axis of the bell-shaped body. In such simple Peritricha as Vorticella, division proceeds until two zooids are produced on a single stalk; one of the two then acquires a second circlet of cilia near its proximal end, becomes

detached (E^3), and, after leading a free-swimming life for a time, settles down and develops a stalk: in this way the dispersal of the non-locomotive species is ensured. In many species of *Zoothamnium* (Fig. 79) the zooids are *dimorphic*: the ordinary bell-shaped forms (*n. z.*) divide in the usual way, but as they remain attached, the process results only in the increased complexity of the colony, not in the development of a new one. The larger zooids (*r. z.*) are globular and mouthless: they become detached, swim off, and, after a short free existence, settle down, develop a stalk (*F*), divide, and so form a new colony.

Cyst-formation takes place in *Colpoda*. The holotrichous Ciliate becomes

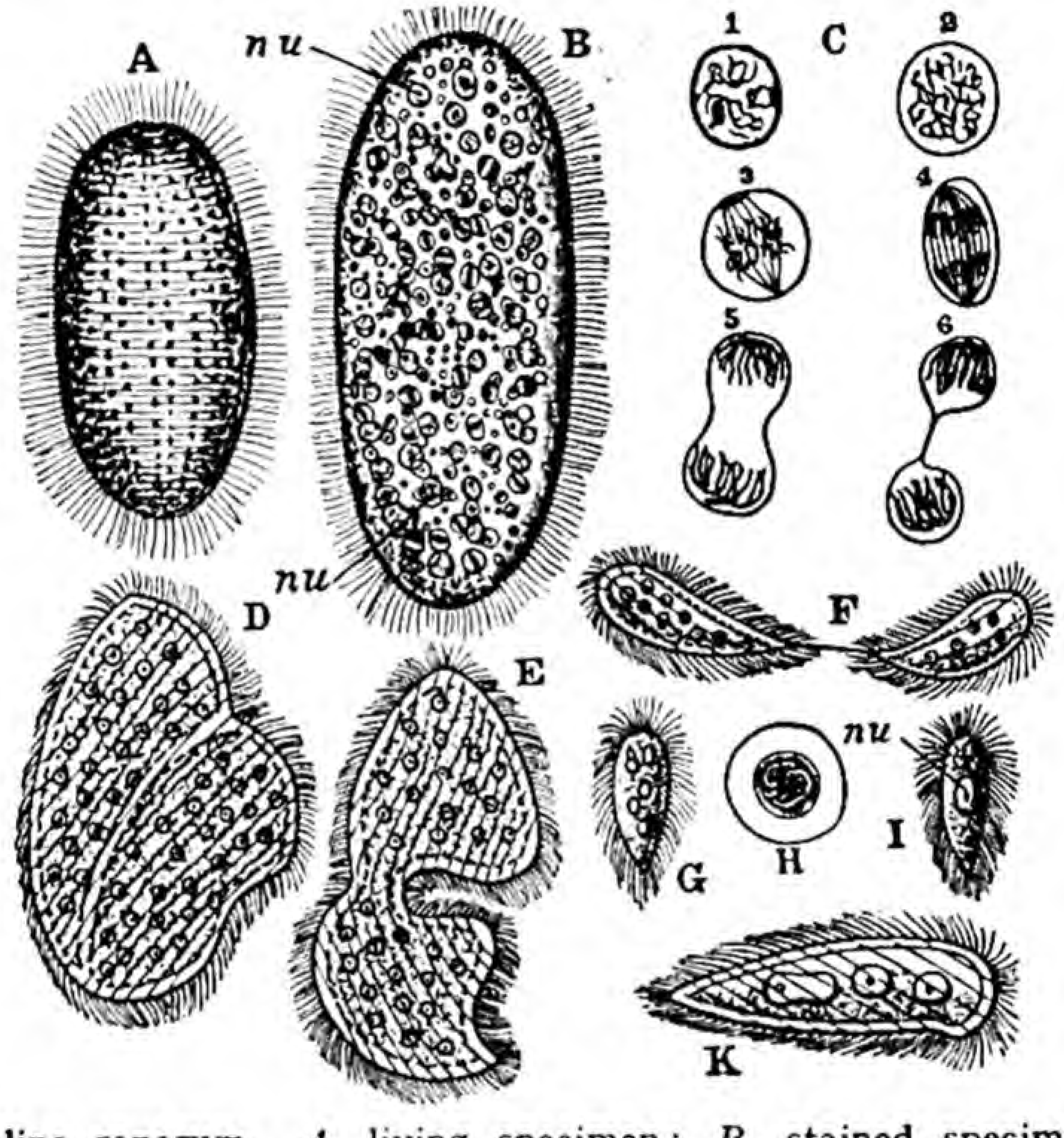


FIG. 80.—**Opalina ranarum.** *A*, living specimen; *B*, stained specimen showing nuclei; *C*, stages in nuclear division; *D—F*, stages in fission; *G*, final product of fission; *H*, encysted form; *I*, gamete liberated from cyst; *K*, zygote after multiplication of the nucleus has begun; *nu*. nucleus. (From Parker's *Biology*, after Saville Kent and Zeller.)

encysted, and divides into two, four, and finally eight masses, each of which, on being liberated, gives rise to a new individual. A somewhat similar process has been described in Vorticella and others.

A peculiar kind of reproduction, specially adapted to the requirements of an internal parasite, takes place in *Opalina* (Fig. 80), a parasite in the intestine of the Frog. Binary fission (*plasmotomy*) takes place (*D*, *E*, *F*), and is repeated again and again so rapidly that the daughter-cells are unable to grow to the adult size before the next division. The final results of the process are small bodies (*G*), each with only three to six nuclei instead of the large number characteristic of the adult. These become encysted (*H*), and in this passive

condition are passed out of the Frog's intestine with its fæces, frequently being deposited on water-weeds. All this takes place during the Frog's breeding season: the tadpoles or Frog-larvæ feed upon the water-plants, and in doing so frequently take in the encysted Opalinæ along with their food. When this occurs the cyst is dissolved by the digestive juices of the host, and the liberated individual becomes divided up into club-shaped bodies, each with a single nucleus (*I*). These are gametes, which copulate in pairs, the zygotes growing into adult Opalinæ (*K*).

Conjugation, in the form of a temporary union accompanied by interchange of micronuclei, has been described in Paramecium (p. 89), and takes place in many Ciliata. In others (*e.g.*, *Stylonychia histrio*) there is a complete union (*copulation*) of the two gametes. In Vorticella union is also permanent, and takes place, not between two ordinary forms, but between one of the ordinary stalked individuals or macrogametes, and a free-swimming, small form or microgamete, produced a number together from one of the fixed individuals by a process of multiple fission. After complicated changes in the nuclei of the two conjugating individuals, during which the microgamete contributes a micronucleus towards the formation of the new nuclear apparatus of the macrogamete, the former shrivels and dies (G^1, G^2). The essence of conjugation is the reception of nuclear material derived from another individual: its effect appears to be a renewal of vitality, usually manifesting itself in increased activity in multiplication by fission.

Though most Ciliata are free, many are parasites, mainly in the alimentary canal of various Metazoa. Pathogenic forms are almost unknown.

Sub-class II.—Suctoria.

Judged from the adult structure alone, the members of this sub-class would certainly be placed in a separate class of the Protozoa: it is only in virtue of the facts of development that they are united in a single class with the Ciliophora.

The **body** may be globular (Fig. 81, *1a*), ovoid (*1b*), or cup-shaped (*2a*), but presents nothing like the variety of form met with among the Ciliata. The distinguishing feature of the group is furnished by the **tentacles** which are always present in greater or less number, and which, in some cases at least, are the most highly differentiated organs found in the whole group of Protozoa. The characters of the tentacles vary strikingly in the different genera.

In the common forms *Podophrya* (*1*), and *Acineta* (*2*), the tentacles spring either from the whole surface, or in groups from the angles of the somewhat triangular body. Each tentacle is an elongated cylindrical structure (*1c*), capable of protrusion and retraction, and having its distal end sucker-like. It is, moreover, practically tubular, the axial region consisting of a semi-fluid protoplasm, while the outer portion is tolerably firm and resistant. When

partially retracted, a spiral ridge is sometimes observable around the tentacle: this may indicate the presence of a band of specially contractile protoplasm,

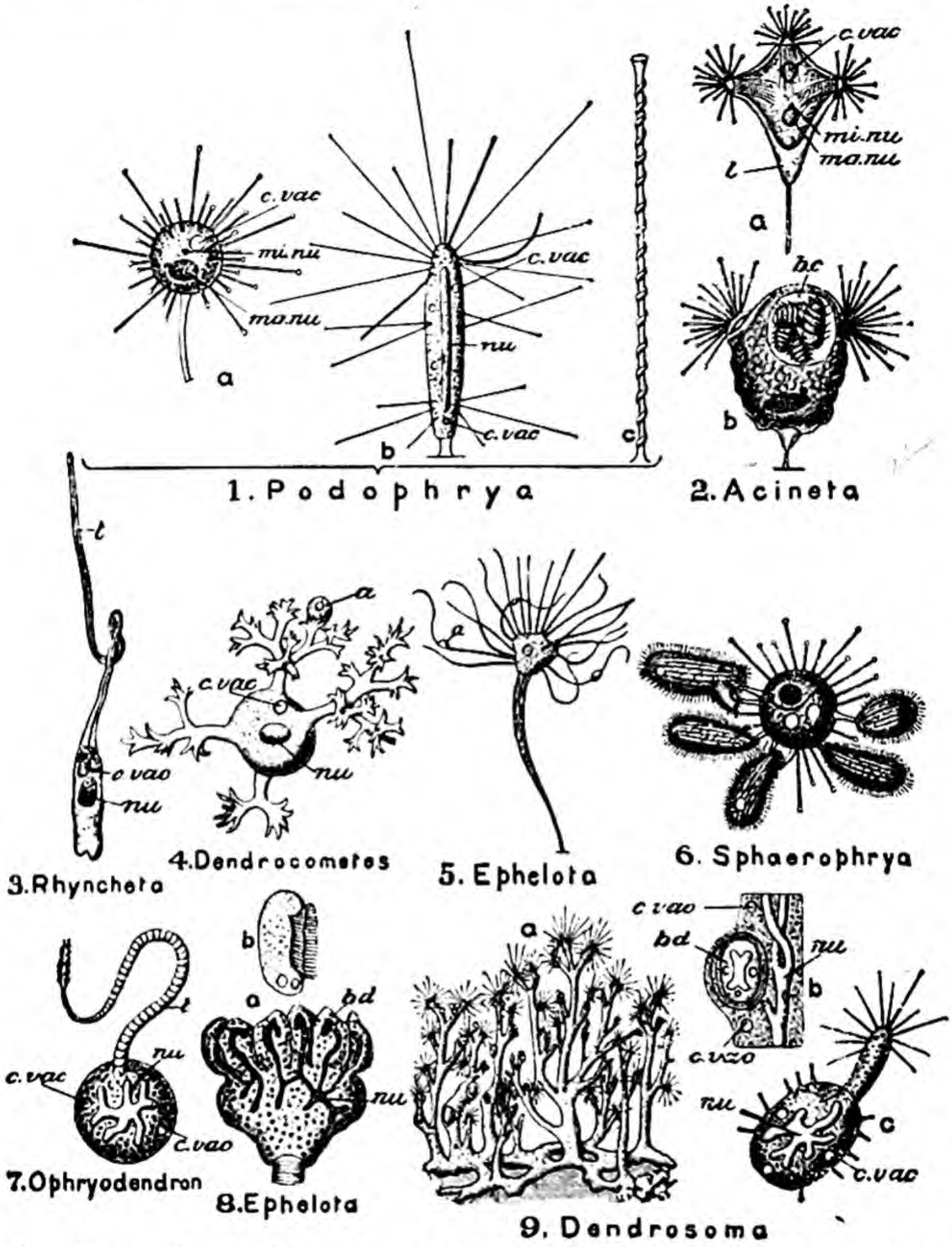


FIG. 81.—Various forms of **Suctoria.** *1a* and *b*, two species of *Podophrya*; *c*, a tentacle much enlarged; *2a*, *Acineta jolyi*; *2b*, *A. tuberosa*; in *6* the animal has captured several small Ciliata; *8a*, a specimen multiplying by budding; *8b*, a free ciliated bud; *9a*, the entire colony; *9b*, a portion of the stem; *9c*, a liberated bud; *a*, organism captured as food; *b.c.* brood-cavity; *bd.* bud; *c. vac.* contractile vacuole; *l.* lorica; *ma.nu.* macronucleus; *mi.nu.* micronucleus; *t.* tentacle. (After Bütschli and Saville Kent.)

resembling the axial myoneme-fibre in the stalk of *Vorticella.* Ciliata and other organisms are caught by the tentacles (*4, 6*), the cuticle of the prey is pierced or dissolved where the sucker touches it, and the semi-fluid protoplasm

can then be seen flowing down the tentacle into the body of the captor. A single tentacle only may be present (*3*), or the tentacle may be branched (*4*), the extremity of each branch being suctorial. In some forms there are no terminal suckers (*5*), and the tentacles are waved about to catch the prey instead of standing out stiffly as in Acineta. In other cases there are one or more long, striated tentacles with tufted ends (*7*).

The **nucleus** may be ovoid (*1a*), horseshoe-shaped, or branched (*8*, *9*): in many cases a micronucleus (*1a*, *mi. nu.*) has been found, and it probably occurs in all. There are one or more **contractile vacuoles** (*c. vac.*).

Some genera are naked (*1*): others form a stalked **shell** or *lorica* (*2a*) like that met with in many of the Mastigophora.

The only **colonial form** is the wonderful *Dendrosoma* (*9*), in which the entire colony attains a length of about 2 mm., and bears an extraordinary resemblance to a zoophyte (*vide* Section IV). It consists of a creeping stem from which vertical branches spring, and the various ramifications of these are terminated in Podophrya-like zooids with suctorial tentacles. The macronucleus is very remarkable, extending as a branched axis throughout the colony (*b*, *nu.*). Micronuclei of the ordinary character are present as well.

Reproduction by *binary fission* takes place in many species. In *Ephelota gemmipara* (*8*) a peculiar process of *budding* occurs: the distal end of the organism grows out into a number of projections or buds, into which branches of the nucleus extend. These become detached, acquire cilia on one surface, and swim off (*b*). After a short active existence tentacles appear and the cilia are lost. In this case budding is external, but in *Acineta tuberosa* (*2b*) the buds become sunk in a depression, which is finally converted into a closed *brood-cavity* (*b.c.*): in this the buds take on the form of ciliated embryos, which finally escape from the parent. In *Dendrosoma* the common stem of the colony produces internal buds (*9*, *b*, *bd.*).

Further Remarks on the Protozoa.

The majority of the Protozoa are aquatic, the phylum being equally well represented in fresh- and salt-water. They occur practically at all heights and depths, from 8000 to 10,000 feet above sea-level to a depth of from 2000 to 3000 fathoms. Some forms, such as species of Amœba and Allogromia, live in damp sand and moss, and may therefore be almost considered as terrestrial organisms. In accordance with their small size and the readiness with which they are transported from place to place, a large proportion of genera and even of species is universally distributed, being found in all parts of the world where the microscopic fauna has been investigated.

Numerous parasitic forms are known. Besides the entire class of Sporozoa, species of Rhizopoda, Mastigophora, and Ciliophora occur both as internal and external parasites.

In each division of the Protozoa we have found comparatively low or generalized forms side by side with comparatively high or specialized genera. For instance, among the Rhizopoda, there can be no hesitation in placing the Lobosa at the bottom of the list, and the Radiolaria at the top. Similarly, among the Mastigophora, the Chrysomonadina have been considered to be the lowest forms, Noctiluca and the Dinoflagellata the highest. But whether the Rhizopoda, as a whole, are higher or lower than the Mastigophora is a question by no means easy to answer. A flagellum certainly seems to be a more specialized cell-organ than a pseudopod, and some of the Mastigophora rise above the highest of the Rhizopoda in the possession of a firm cortex and cuticle, and the consequent assumption of a more definite form of body than can possibly be produced by the flowing protoplasm of a Foraminifer or a Radiolarian. On the other hand, the nucleus of the Radiolaria is a far more complex structure than that of the Mastigophora; and in Foraminifera, Radiolaria, and Heliozoa the organism frequently begins life as a flagellula, a fact which, on the hypothesis that the development of the individual recapitulates that of the race, appears to indicate that these orders of Rhizopoda are a more recently developed stock than at any rate the lower Flagellata. These circumstances, and the fact that Mastigamœba might equally well be classed as a lobose Rhizopod with a flagellum or as a Flagellate with pseudopods, seem to indicate that the actual starting-point of the Protozoa was a form capable of assuming either the amœboid or the flagellate phase. From such a starting-point the Lobosa, Foraminifera, Heliozoa, Radiolaria, and Mastigophora diverge in different directions, the first four keeping mainly to the amœboid form, but assuming the flagellate form in the young condition in the case of Foraminifera, Heliozoa, and Radiolaria.

The Choanoflagellata, Dinoflagellata, and Cystoflagellata are obviously special developments of the flagellate type along diverging lines.

As to the Ciliata, *Multicilia* (Fig. 76, *12*) appears to indicate the derivation of the order from the flagellate type, since its cilia are long and flagellum-like. The derivation of the Suctoria from a ciliate type appears to be clear. The Suctoria and the hypotrichous Ciliata are undoubtedly the highest development of the Protozoan series, since they show a degree of differentiation attained nowhere else in this phylum.

The Mycetozoa appear to have been derived from the common amœboid-flagellate stock, since they are all predominantly amœboid in the adult condition, flagellate when young. The Sporozoa probably had a similar origin, but the characters of this class have evidently been profoundly modified in accordance with their parasitic mode of life.

SECTION III

SUB-KINGDOM PARAZOA

PHYLUM AND CLASS PORIFERA

THE microscopic animals described in the preceding section are, as already pointed out, distinguished by their *non-cellular* character, and in this respect stand in contrast to the remainder of the animal kingdom, the members of which are characterized by a *cellular* structure of their body. For reasons to be discussed later (Section IV, p. 214), the cellular animals are subdivided further into separate sub-kingdoms, the *Parazoa* and the *Metazoa*. Owing to a high degree of uniformity in the principles of structure among the representatives of the Parazoa, only one phylum, the Porifera or Sponges, and one class of the same name is recognized.

1. EXAMPLE OF THE CLASS—*Sycon gelatinosum*.

General External Appearance and Gross Structure.—*Sycon gelatinosum*,[1] one of the Calcareous Sponges, has the form of a tuft, one to three inches long, of branching cylinders (Fig. 82), all connected together at the base, where it is attached to the surface of a rock or other solid body submerged in the sea. It is flexible, though of tolerably firm consistency; in colour it presents various shades of grey or light brown. To the naked eye the surface appears smooth, but when examined under the lens it is found to exhibit a pattern of considerable regularity, formed by the presence of innumerable elevations of a polygonal shape, which cover the whole surface and are separated off from one another by a system of depressed lines. In these depressions between the elevations are to be detected, under the microscope, groups of minute pores—the *ostia* or inhalant pores. At the free end of each of the cylindrical branches is a small but distinct opening, surrounded by what appears like a delicate fringe. When the branches are bisected longitudinally (Fig. 83), it is found that the terminal openings (*o.*) lead into narrow passages, wide enough to admit a stout pin,

FIG. 82.—**Sycon gelatinosum.** Entire sponge, consisting of a group of branching cylinders (natural size).

[1] This species is an inhabitant of southern seas. In all essential respects the account of it given above will apply to *S. ciliatum*, a common European species which differs chiefly in the absence of the pore-membranes.

running through the axes of the cylinders; and the passages in the interior of the various branches join where the branches join—the passages thus forming a communicating system. On the wall of the passages are numerous fine apertures which require a strong lens for their detection. The larger apertures at the ends of the branches are the *oscula* of the sponge, the passages the *paragastric cavities*. If a living Sycon is placed in sea-water with which has been mixed some carmine powder, it will be noticed that the minute particles of the carmine seem to be attracted towards the surface of the sponge, and will often be seen to pass into its substance through the minute inhalant pores or ostia already mentioned as occurring in groups between the elevations on the outer surface. This would appear to be due to the passage of a current of water into the interior of the sponge through these minute openings dotted over the surface; and the movement of the floating particles shows that a current is at the same time flowing out of each of the oscula. A constant circulation of water would thus be seen to be carried on—currents moved by some invisible agency flowing through the walls of the sponge to the central paragastric cavities, and passing out again by the oscula.

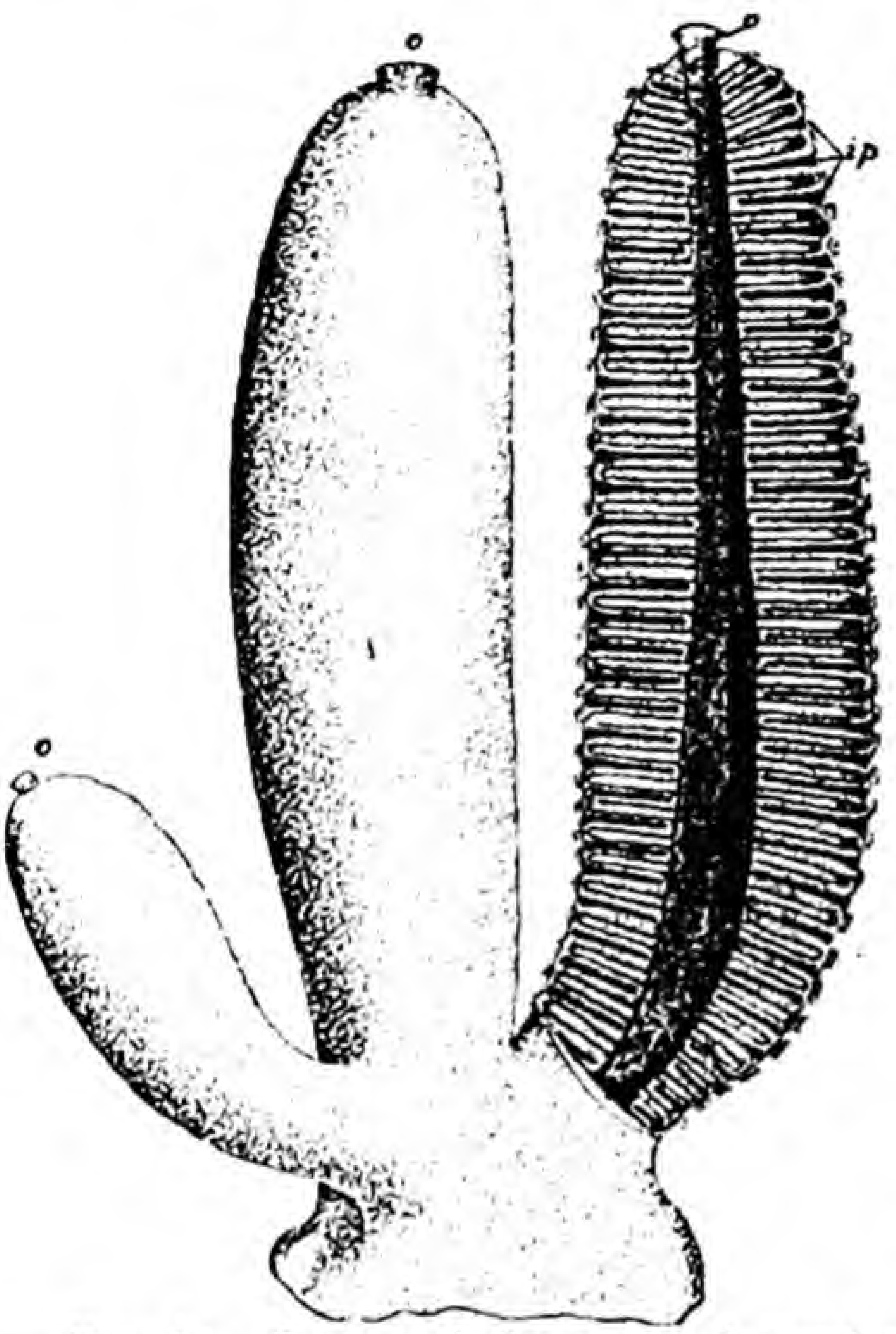


FIG. 83.—**Sycon gelatinosum.** A portion slightly magnified; one cylinder (that to the right) bisected longitudinally to show the central paragastric cavity opening on the exterior by the osculum, and the position of the incurrent and radial canals; the former indicated by the black bands, the latter dotted; *ip*, marks the position of three of the groups of inhalant pores at the outer ends of the incurrent canals; *o*, osculum.

If a portion of the Sycon is firmly squeezed, there will be pressed out at first sea-water, and then, when greater pressure is exerted, a quantity of gelatinous-looking matter, which, on being examined microscopically, proves to be partly composed of a protoplasmic material consisting of innumerable usually more or less broken cells with their nuclei, and partly of a non-protoplasmic, jelly-like substance. When this is all removed there remains behind a toughish felt-like material, which maintains more or less completely the original shape of the sponge. This is the *skeleton* or supporting framework. A drop of acid causes it to dissolve with effervescence, showing that it consists of carbonate of lime. When some of it is teased out and examined under the microscope, it proves to consist of innumerable, slender, mostly three-rayed

microscopic bodies (Figs. 84 and 85, *sp.*) of a clear glassy appearance. These are the *calcareous spicules* which form the skeleton of the Sycon.

The arrangement of the spicules, their relation to the protoplasmic parts, and the structure of the latter, have to be studied in thin sections of hardened specimens (Figs. 84 and 85). An examination of such sections leads to the following results.

Microscopic Structure.—Covering the outer surface of the sponge is a single layer of cells—the *dermal layer* (Fig. 85, *ec.*)—through which project regularly-arranged groups of needle-like and spear-like spicules (*sp'.*), forming the pattern of polygonal elevations on the outer surface. The cells of the ectoderm (*pinacocytes*) are in the form of thin scales, which are closely cemented together

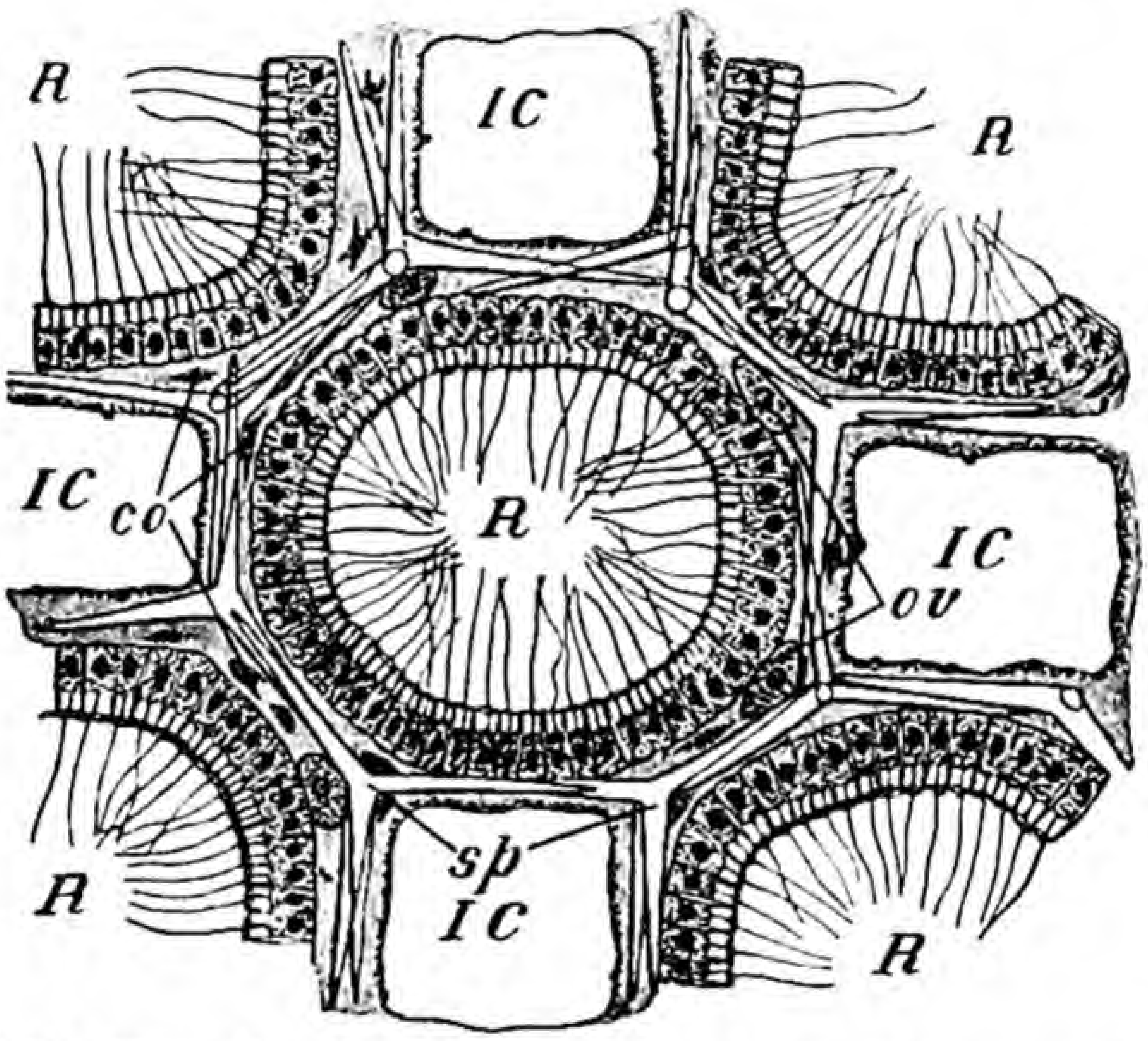


FIG. 84.—**Sycon gelatinosum.** Section through the wall of a cylinder taken at right angles to the long axes of the canals, highly magnified; *co.* collencytes; *IC.* incurrent canals; *ov.* young ova; *R.* radial canals; *sp.* triradiate spicules.

by their edges. The paragastric cavities are lined by a layer of cells (*en.*) which are, like those of the ectoderm, thin flattened scales. Running radially through the thick wall of the cylinders are a large number of regularly-arranged straight passages. Of these there are two sets, those of the one set—the *incurrent canals* (Figs. 84 and 85, *IC.*)—narrower, and lined by ectoderm similar to the ectoderm of the surface; those of the other set—the *radial* or *flagellate canals* (*R.*)—rather wider, octagonal in cross-section, and lined by the gastral layer continuous with the lining of the paragastric cavity. The incurrent canals end blindly at their inner extremities—not reaching the paragastric cavity; externally each becomes somewhat dilated, and the dilatations of neighbouring canals often communicate. These dilated parts are closed externally by a thin membrane—the *pore-membrane* (Fig. 85, *p.m.*,

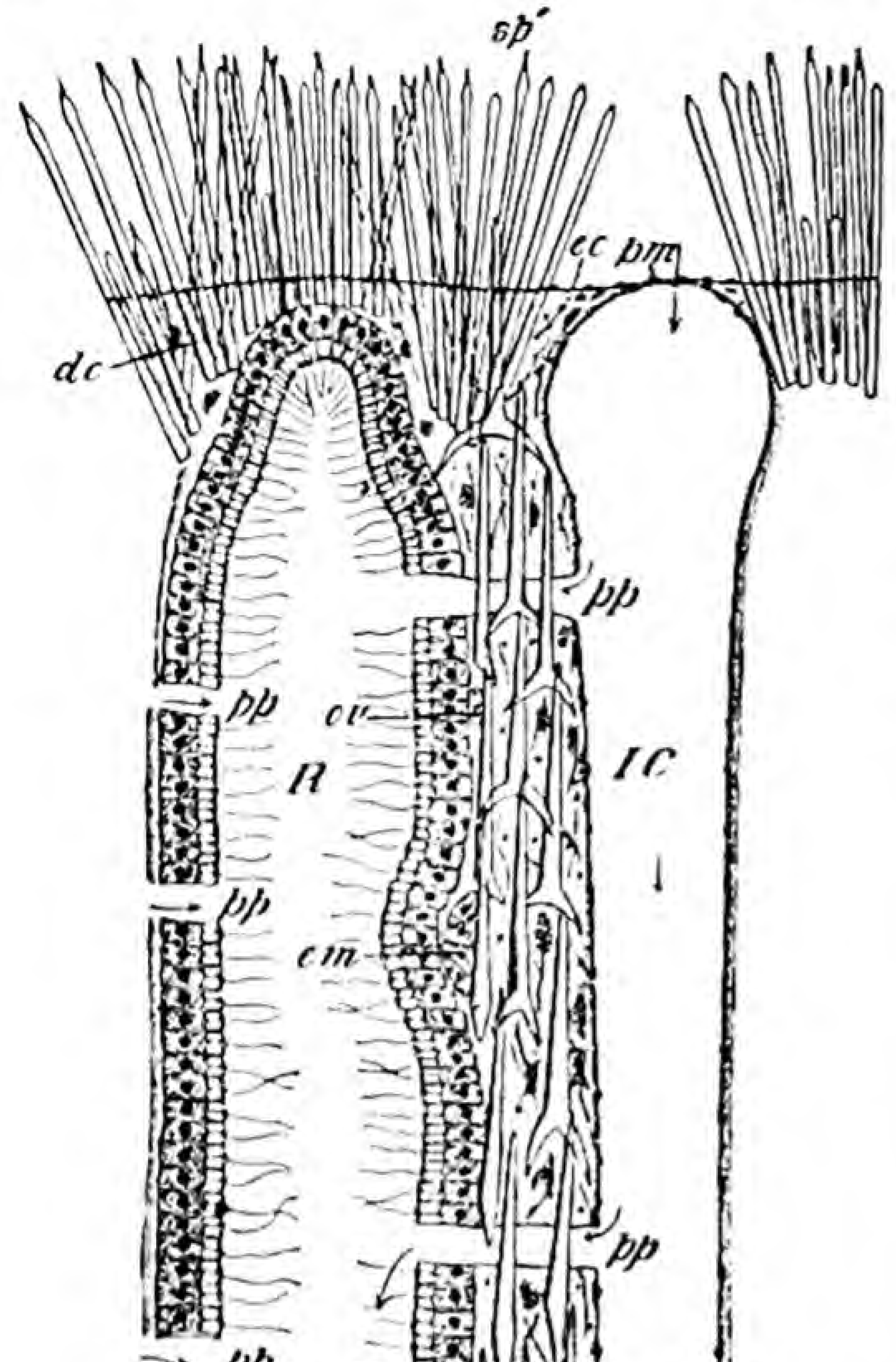


FIG. 85.—**Sycon gelatinosum.** Transverse section through the wall of a cylinder (parallel with the course of the canals), showing one incurrent (*IC.*), and one radial (*R.*) canal throughout their length; *sp.* triradiate spicules; *sp'.* oxeote spicules of dermal cortex (*dc.*); *sp''.* tetraradiate spicules of gastral cortex (*gc.*); *ec.* dermal layer; *en.* gastral layer of flattened cells lining the paragastric cavity; *p.m.* pore-membrane; *pp.* prosopyles; *ap.* apopyle; *di.* diaphragm; *exc.* excurrent passage; *P.G.* paragastric cavity; *em.* early embryo; *em'.* late embryo. The arrows indicate the course of the water through the sponge.

and Fig. 86), perforated by three or four small openings (Fig. 86, *p.*)—the ostia already referred to. The flagellate canals are blind at their outer ends, which lie at a little distance below the surface opposite the polygonal projections referred to above as forming a pattern on the outer surface; internally, each communicates with the paragastric cavity by a short, wide passage—the *excurrent canal* (Fig. 85, *exc.*). Incurrent and flagellate canals run side by side, separated by a thin layer of sponge substance except at certain points, where there exist small apertures of communication—the *prosopyles* (*pp.*)—uniting the cavities of adjacent incurrent and flagellate canals. Each prosopyle is a perforation in a single cell termed a *porocyte.*

The dermal layer lining the incurrent canals is of the same character as that of the outer surface. The cell-layer lining the flagellate canals, on the other hand, is totally different from that which lines the paragastric cavity. It consists of cells of columnar shape ranged closely together so as to form a continuous layer. Each of these flagellate *gastral cells*, or *collared cells*, or *choanocytes*, as they are termed, is not unlike one of the choanoflagellate Protozoa; it has a nucleus, one or more vacuoles, and, at the inner end, a single, long, whip-like flagellum, surrounded at its base by a delicate, transparent, collar-like upgrowth, similar to that which has

already been described as occurring in the Choanoflagellata. If a portion of a living specimen of the sponge is teased out in sea-water, and the broken fragments are examined under a tolerably high power of the microscope, groups of these collared cells will be detected here and there, and in many places the movement of the flagella will be readily observed. The flagellum is flexible but with a certain degree of stiffness, especially towards the base, and its movements resemble those which a very supple fishing-rod is made to undergo in the act of casting a long line—the movement being much swifter and stronger in the one direction than in the other. The direction of the stronger movement is seen, when some of the cells are observed in their natural relations, to be from without inwards. It is to these movements that the formation of the currents of water passing along the canals is due. The collars of the cells in specimens teased in this way become for the most part drawn back into the protoplasm.

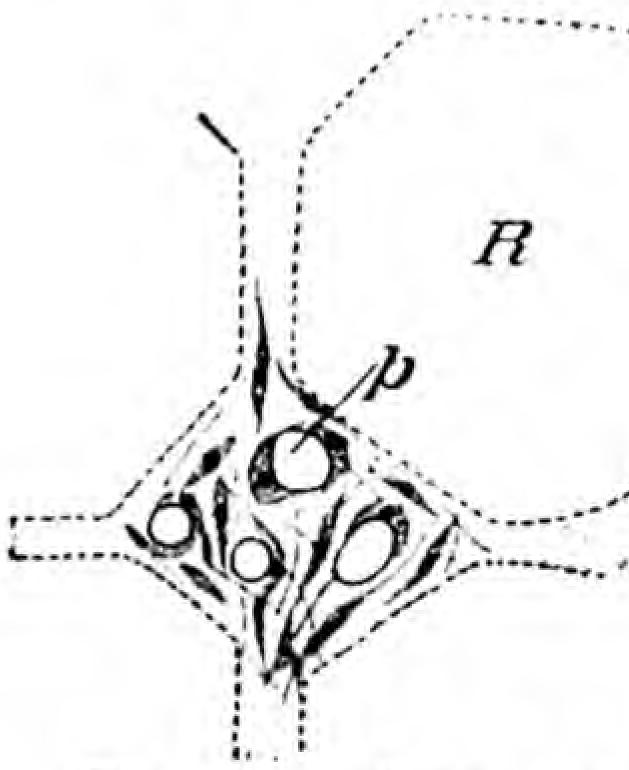


FIG. 86.—**Sycon gelatinosum.** Surface view of a pore-membrane highly magnified; *p.* ostium; *R.* position of the outer end of a radial canal.

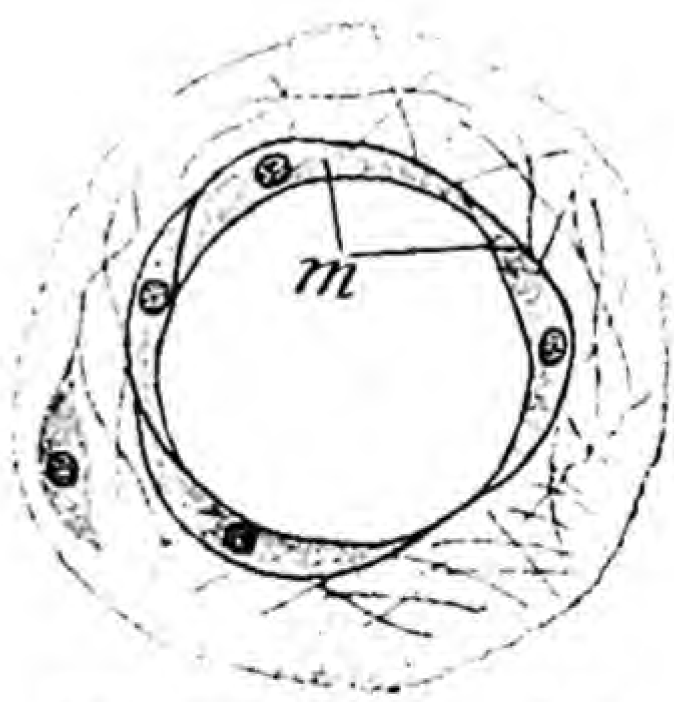


FIG. 87.—**Sycon gelatinosum.** An apopyle surrounded by its diaphragm; *m.* contractile cells.

The short passage or excurrent canal, which leads inwards from the flagellate canal to the paragastric cavity, differs from the former in being lined by flattened cells similar to those of the paragastric cavity; it is partly separated from the flagellate canal by a thin diaphragm (Fig. 85, *di.*, and Fig. 87), perforated by a large circular central aperture—the *apopyle* (*ap.*)—which is capable of being contracted or dilated: its opposite aperture of communication with the paragastric cavity, which is very wide, is termed the *gastric ostium* of the excurrent canal.

The effect of the movement of the flagella of the cells in the flagellate canals is to produce currents of water running from without inwards along the canals to the paragastric cavity. This causes water to be drawn inwards through the prosopyles from the incurrent canals, and, indirectly, from the exterior through the perforated membranes at the outer ends of the latter.

Between the epithelial layer covering the outer surface and the incurrent canals, and the gastral layer of the inner surface and of the flagellate canals,

are a number of spaces filled by an intermediate layer—in which the spicules of the skeleton are embedded. Each spicule is developed from cells termed *scleroblasts*, which migrate inwards from the dermal epithelium. Each ray is formed by the agency of a separate scleroblast, so that there are three at least of the latter for each triradiate, and four for each tetraradiate spicule. The spicules (Figs. 84, and 85, *sp.*) are regularly arranged, and connected together in such a way as to protect and support the soft parts of the sponge. Most are, as already noticed, of triradiate form. Large numbers, however, are of simple spear-like or club-like shape (*sp'.*); these, which are termed the *oxeote spicules*, project on the outer surface beyond the ectoderm, and are arranged in dense masses, one opposite the outer end of each of the flagellate canals, this arrangement producing the pattern already referred to as distinguishable on the outer surface. The thick outer layer in which the bases of these oxeote spicules lie embedded is termed the *dermal cortex* (*dc.*). A thick stratum at the inner ends of the canals and immediately surrounding the paragastric cavity is termed the *gastral cortex* (*gc.*). It is supported by triradiate and also by tetraradiate spicules, one ray of each of which (*sp''.*) frequently projects freely into the paragastric cavity, covered over by a thin layer of flattened gastral cells.

The intermediate layer itself, as distinguished from the spicules which lie embedded in it, consists of a clear gelatinous substance containing numerous nucleated cells of several different kinds. Most of these are small cells of stellate shape, with radiating processes—the *connective-tissue cells* or *collencytes* (Fig. 84, *co.*); others are fusiform; a good many—the amœboid *wandering cells*—are Amœba-like, and capable of moving about from one part of the sponge to another. Their function is the transport of food substances and excreta.

Around the inhalant pores and the apopyles are elongated cells (Figs. 86 and 87), sometimes prolonged into narrow fibres. These are contractile—effecting the closure of the apertures in question—and are therefore to be looked upon as of the nature of *muscular fibres*. A band of similar fibres surrounds the osculum—the *oscular sphincter*.

The sexual reproductive cells—the ova (Figs. 84 and 85, *ov.*) and sperms —are developed immediately below the epithelium of the flagellate canals, and in the same situation are to be found developing embryos (*em.*, *em'.*), resembling in their various stages those of *Sycon raphanus*, as described below.

2. Distinctive Characters and Classification.

Sponges are plant-like, fixed, aquatic Metozoa, all, with the exception of one family, inhabitants of the sea. The primary form is that of a vase or cylinder, the sides of which are perforated by a number of pores and in the interior of which is a single cavity; but in the majority of Sponges a process of branching and

folding leads to the formation of a structure of a much more complex character. The skeleton or supporting framework consists in some cases of fine, flexible fibres of a material termed spongin ; *in others of spongin-fibres supplemented by microscopic siliceous spicules ; in others of siliceous spicules alone ; in others of spicules of carbonate of lime. Reproduction takes place both asexually by the formation of* gemmules, *and sexually by means of ova and sperms. The ovum develops into a ciliated free-swimming larva, which afterwards becomes fixed and develops into the plant-like adult Sponge.*

The Sponges are sufficiently far removed in structure from the Metazoa to justify us in looking upon them as constituting a separate sub-kingdom, the Parazoa. At the same time there is so much uniformity of structure within the group that a division into classes is not demanded ; the phylum Porifera contains a single class.

The class Porifera is classified as follows:—

Sub-Class I.—Calcarea.

Sponges with a skeleton of calcareous spicules, and with comparatively large collared cells.

ORDER 1.—HOMOCŒLA.

Calcareous Sponges in which the internal lining membrane consists throughout of flagellate collared cells.

Example : *Clathrina* (Fig. 89).

ORDER 2.—HETEROCŒLA.

Calcareous Sponges in which the paragastric cavity is lined by flattened cells, the collared cells being restricted to flagellate canals or chambers.

Examples : *Sycon* (Fig. 82) ; *Leucilla* (Fig. 90, *C*).

Sub-Class II.—Hexactinellida.

Sponges with six-rayed, tri-axon, siliceous spicules, and simple canal system represented by unbranched or branched flagellate chambers.

Examples : *Euplectella* ; *Pheronema* (Fig. 96) ; *Hyalonema*.

Sub-Class III.—Demospongia.

Sponges either devoid of skeleton or with spongin fibres alone, or a combination of spongin fibres and siliceous spicules, the latter, when present, never six-rayed ; the canal system of the Rhagon type usually complicated.

ORDER 1.—TETRACTINELLIDA.

Demospongia with tetraxon spicules.

Order 2.—Monaxonida.

Demospongia with monaxon spicules.

Examples: *Cliona*; *Poterion* (Fig. 88, *D*); *Spongilla* (Fig. 91); *Pachychalina* (Fig. 94, *B*).

Order 3.—Ceratosa.

Demospongia with skeleton of spongin fibres without siliceous spicules.

Examples: *Euspongia* (Fig. 94, *A*); *Spongelia* (Fig. 94, *C*).

Order 4.—Myxospongia.

Demospongia devoid of skeleton.

Example: *Oscarella*.

3. General Organization.

General Form and Mode of Growth.—The simplest Sponges are vase-shaped or cylindrical in form, either branched or unbranched; and, if branched, with or without anastomosis or coalescence between neighbouring branches. But the general form of the less simple Sponges diverges widely from that of such a branching cylinder as is presented by Sycon gelatinosum (Fig. 82).

From the point to which the embryonic sponge becomes attached it may spread out horizontally, following the irregularities of the surface on which it grows, and forming a more or less closely adherent encrustation like that of an encrusting lichen (Fig. 88, *A*). The surface of such an encrustation may be smooth; more commonly it is raised up into elevations—rounded bosses, cones, ridges or lamellæ; and the edges may be entire or lobed. In other cases the sponge grows at first more actively in the vertical than in the horizontal direction, and the result may be a long, narrow structure, cylindrical or compressed, and more or less branched (Fig. 88, *B*). Sometimes vertical and horizontal growth is almost equal, so that eventually there is formed a thick, solid mass of a rounded or polyhedral shape (Fig. 88, *C*), with an even, or lobed, or ridged surface. Very often, after active vertical growth has resulted in the formation of a comparatively narrow basal part or stalk, the Sponge expands distally, growing out into lobes or branches of a variety of different forms, and frequently anastomosing. Sometimes, after the formation of the stalk with root-like processes for attachment, the Sponge grows upwards in such a way as to form a cup or tube with a terminal opening. Such a cup-shaped Sponge, exemplified in the gigantic Neptune's Cup (*Poterion*, Fig. 88, *D*), is not to be confounded with the simple vase or cup referred to above as the simplest type of Sponge, being a much more complex structure with many oscula. Sometimes the Sponge grows from the narrow base of attachment into a thin flat plate or lamella; this may become divided up into a number of parts or lobes, which

may exhibit a divergent arrangement like the ribs of an open fan. Often the lamella becomes folded, and sometimes there is a coalescence between the folds, resulting in the development of a honeycomb-like form of sponge.

Sponges resemble plants, and differ from the higher groups of animals, in the readiness with which, in many cases, their form becomes modified during growth by external conditions (environment). Different individuals of the same kind of Sponge, while still exhibiting the same essential structure and

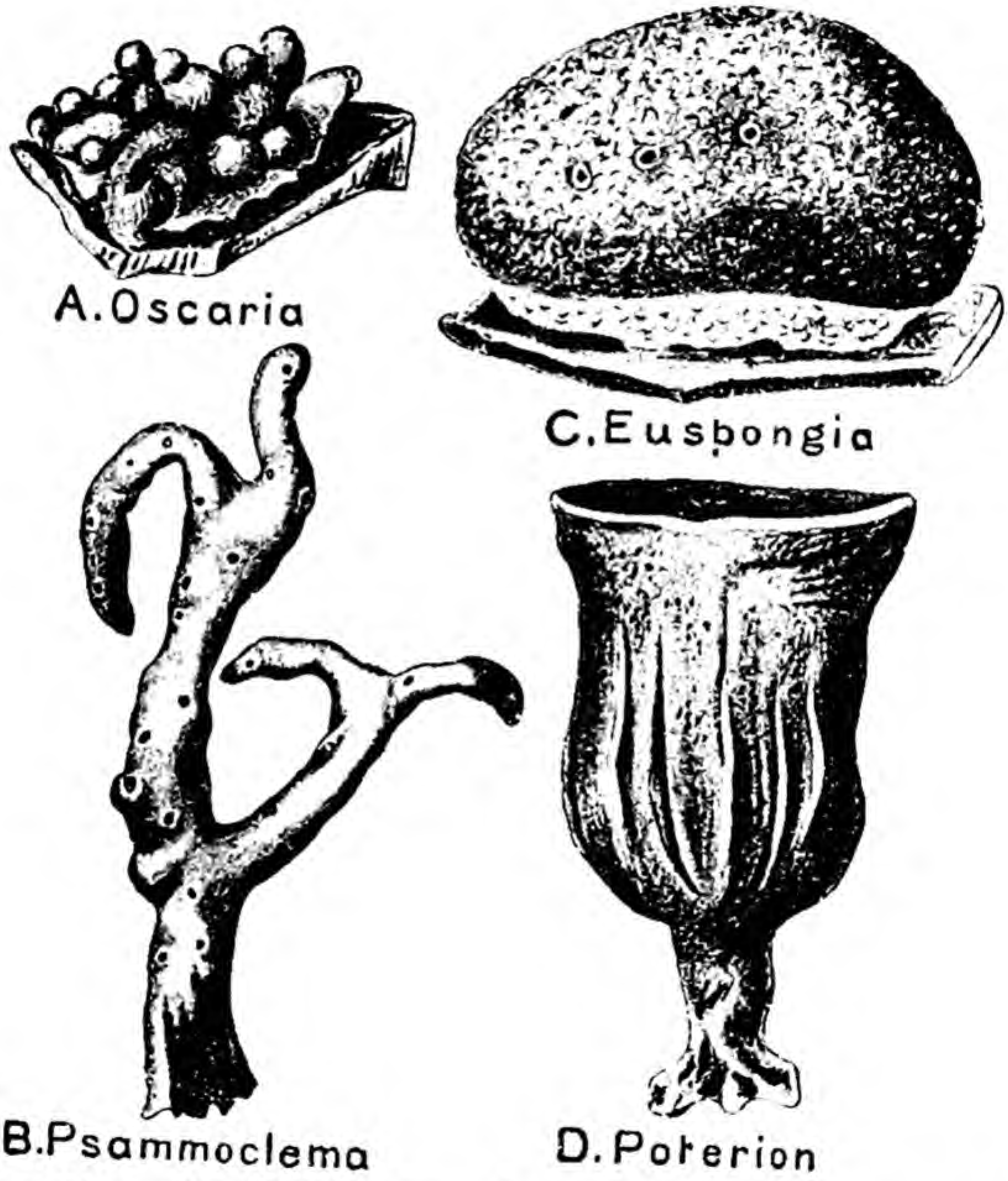


FIG. 88.—External form of various Sponges. *A*, **Oscaria**, an encrusting form, with the upper surface raised up into a number of rounded prominences; *B*, **Psammoclema**, a ramifying sub-cylindrical Sponge; *C*, **Euspongia** (toilet sponge), a massive form with a broad base; *D*, **Poterion** (Neptune's Cup), an example of a complex Sponge assuming the form of a vase. (After Vosmaer.)

the same general mode of growth, may present a variety of minor differences of form, in accordance with differences in the form of the supporting surface or in the action of waves and currents.

Leading Modifications of Structure.—Sycon gelatinosum belongs to a type of Sponges intermediate between the very simplest forms on the one hand and the more complex on the other. The simplest type of Sponge-structure is that of the so-called *Ascetta* or *Olynthus* (Fig. 89). This is not a mature

form—no adult Sponge retaining such simplicity of structure. It is vase-shaped, contracted at the base to form a sort of stalk by the expanded extremity of which it is attached; at the opposite or free end is the circular osculum. So far there is a considerable resemblance to Sycon gelatinosum; but the structure of its wall in Ascetta is extremely simple. Regularly arranged over the surface are a number of small rounded apertures, the inhalant pores; but, since the wall of the Sponge is very thin, these apertures

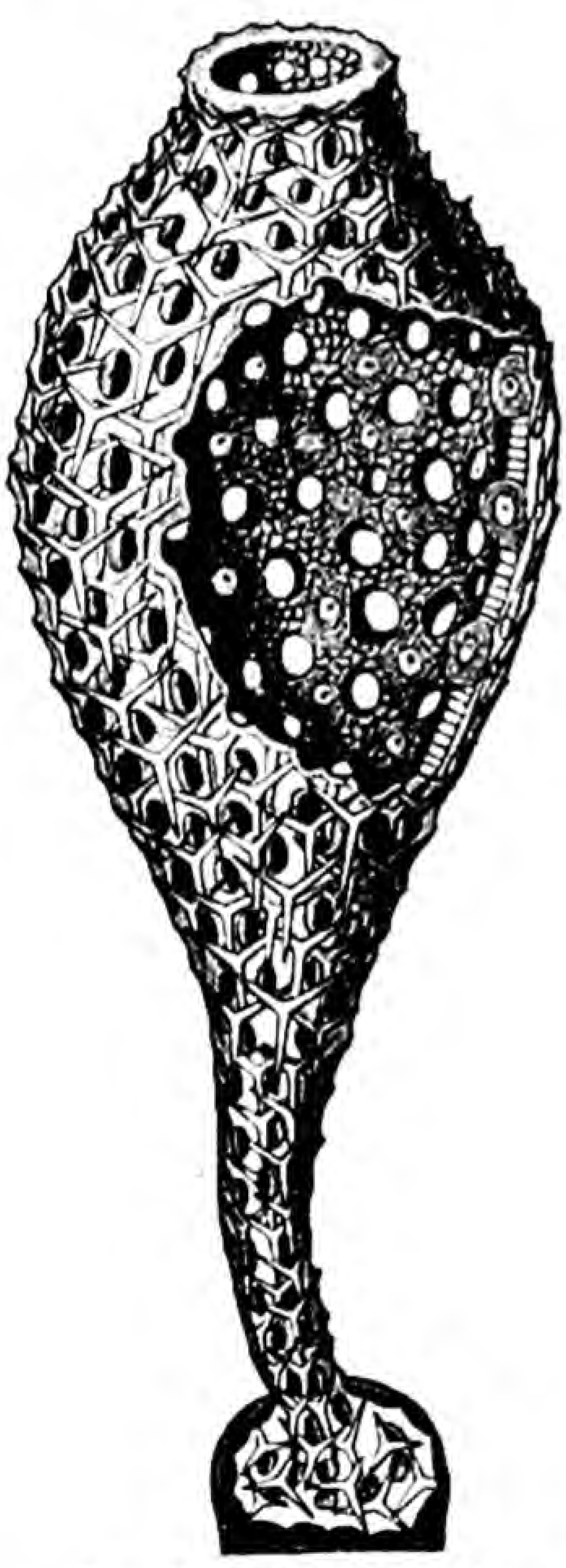


FIG. 89.—**Olynthus** stage of a simple calcareous Sponge (*Clathrina*). A portion of the wall of the vase-like sponge removed to show the paragastric cavity. (After Haeckel.)

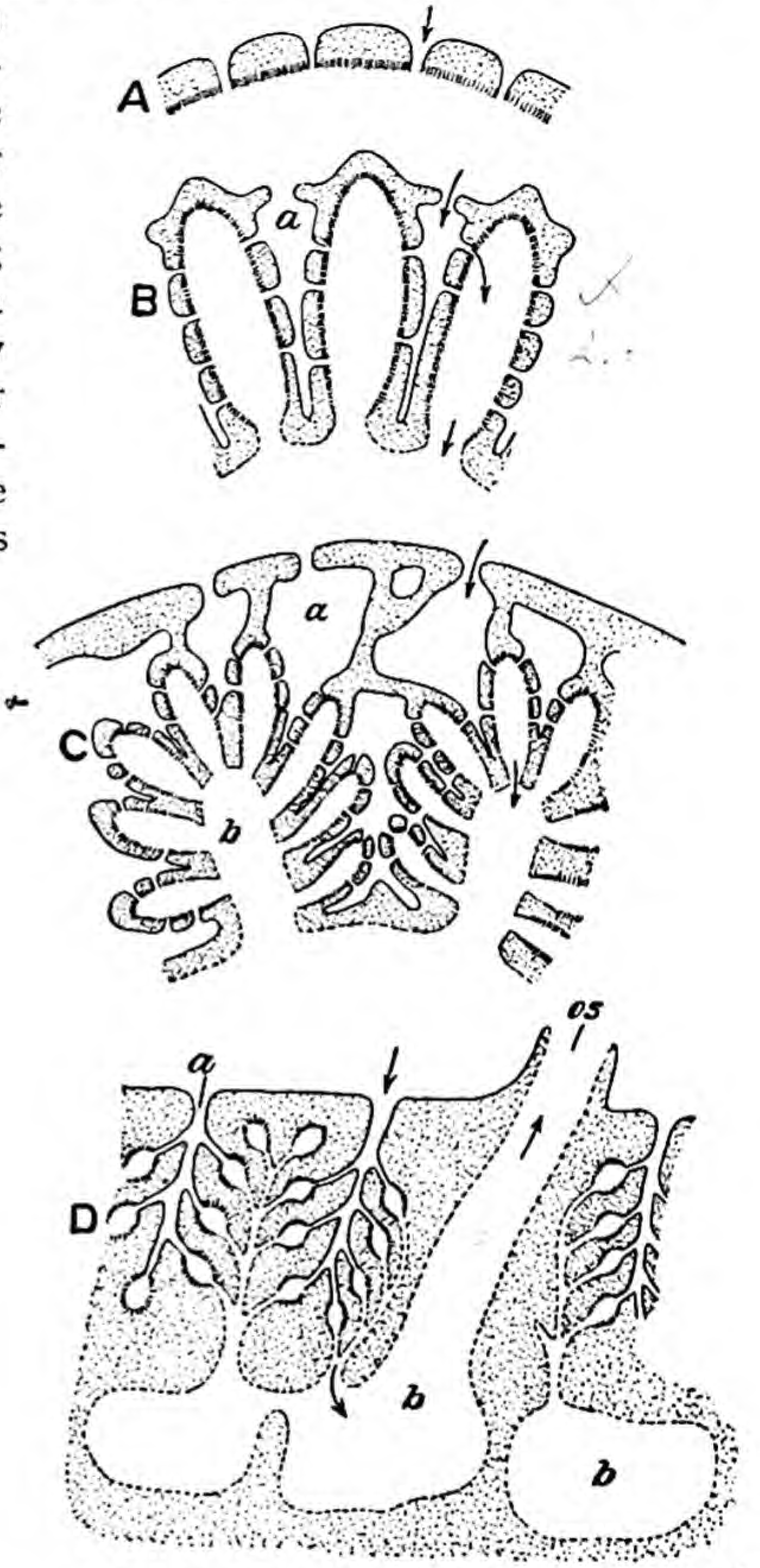


FIG. 90.—Diagram of the canal system of various sponges, the dermal epithelium denoted by a continuous narrow line; the flattened gastral epithelium by an interrupted line; the flagellate gastral epithelium by short parallel strokes. *A*, cross-section through a part of the wall of an Ascon; *B*, cross-section through a part of the wall of a Sycon; *C*, cross-section through a part of the wall of *Leucilla convexa*; *D*, vertical section through *Oscarella*; *a*, spaces of the incurrent canal system; *b*, spaces of the ex-current canal system; *os*. osculum. (After Korschelt and Heider.)

lead directly into the central or paragastric cavity (Fig. 90, *A*), the long passages or canals through which the communication is effected in Sycon being absent. The wall consists of the same three layers as in Sycon, but the middle one, though it contains a small number of spicules, is very thin. The dermal epithelium is a thin layer of flat cells; the paragastric cavity is lined throughout by choanocytes similar to those of the flagellate canals of Sycon. A somewhat more complex type of structure than that of Ascetta is exhibited by those sponges in which the wall becomes thickened and perforated by radially-arranged canals, which open directly on the outer surface by means of *inhalant pores* or *ostia*, and lead directly into the paragastric cavity by means of *apopyles*—the whole inner surface as well as the radial canals being lined with flagellate cells. In forms which may be regarded as representing the next stage of development (Fig. 90, *B*: see also the figures of Sycon gelatinosum), there are formed by infolding

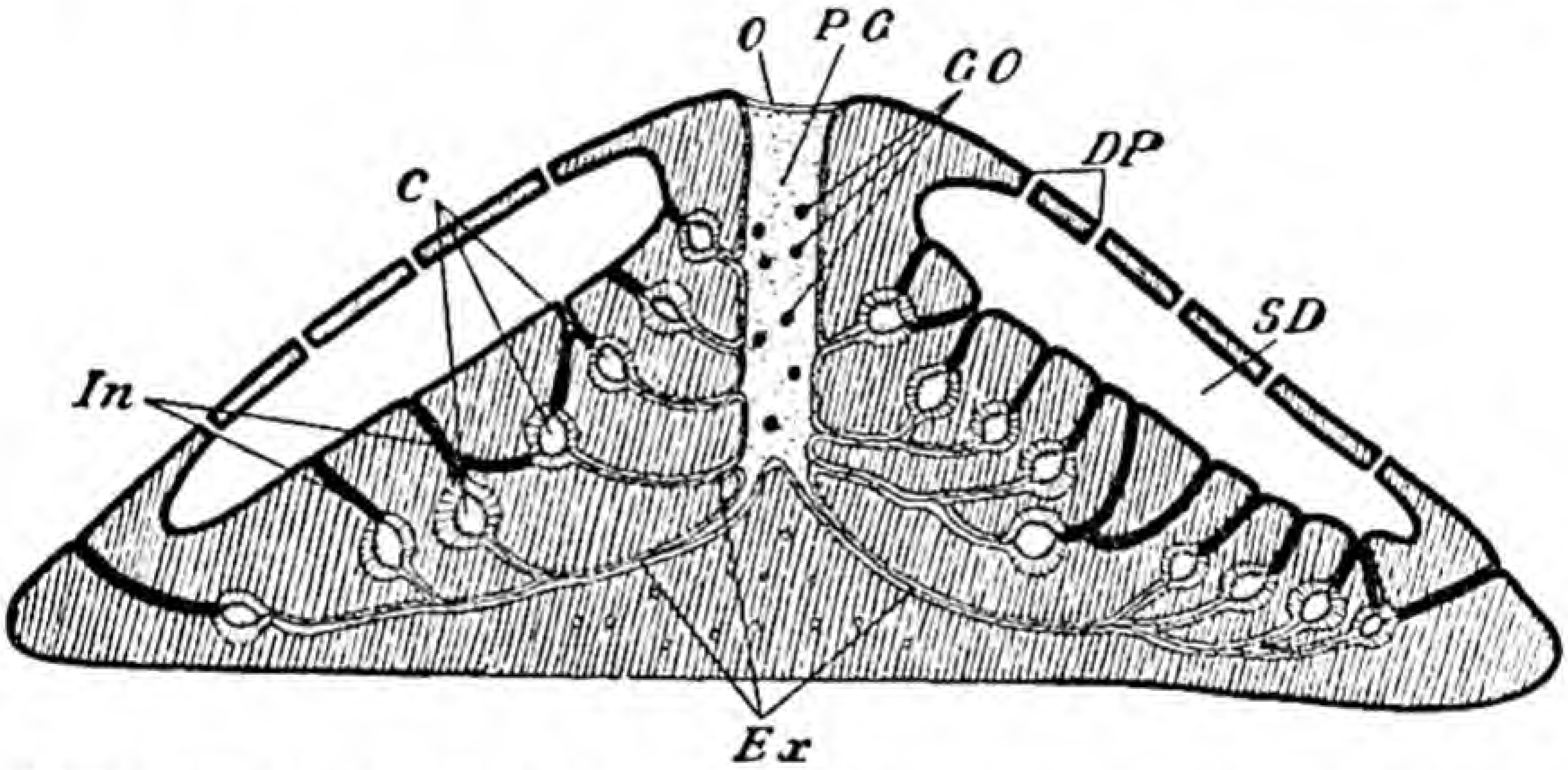


FIG. 91.—Vertical section of a fresh-water sponge (**Spongilla**), showing the arrangement of the canal-system. *C*. ciliated chambers; *DP*. dermal pores; *Ex*. excurrent canals; *GO*. openings of the excurrent canals; *PG*. paragastric cavity; *SD*. subdermal cavities; *O*. osculum. (Modified from Leuckart and Nitsche's diagrams.)

of the surface, in the intervals between the radial canals, canal-like spaces, the *incurrent canals*, lined by dermal epithelium and communicating with the exterior on the one hand, either by a wide opening or by pores (ostia) perforating a pore-membrane, and on the other by means of small openings, the *prosopyles* (the equivalents of the inhalant pores of the *Olynthus*), with the radial canals. Sponges similar to Sycon gelatinosum, but with flagellate canals arranged in groups, each group centred round a main excurrent canal (Fig. 90, *C*), afford us the next grade of advancing complexity. In these the incurrent canals may form a branching system. In all the higher groups of Sponges (Fig. 90, *D*, and Fig. 91) the flagellate cells are confined to certain special enlargements of the canals—the so-called "ciliated chambers" (*C*)—and the rest of the canals are lined by flattened cells.

Special names have been applied to the main types of canal-system briefly sketched above. Forms in which the paragastric cavity is lined by flagellate

cells are said to belong to the *Ascon* type, whether the paragastric cavity communicates directly or by flagellate canals with the exterior. Forms in which there is a paragastric cavity lined by flattened cells, and a system of radially arranged flagellate chambers, are said to possess the *Sycon* type of structure. Such Sponges as have small rounded flagellate chambers (" ciliated chambers "), communicating in most cases by narrow branching incurrent canals with the exterior (directly or indirectly) on the one hand, and by similar excurrent canals with the paragastric cavity on the other—the flagellate cells being confined to the flagellate chambers—are said to possess the *Rhagon* type of canal-system. In the *Rhagon* proper the arrangement of parts is very simple. The Sponge has a paragastric cavity opening on the exterior by an osculum. Opening into this central cavity by wide apopyles are a number of rounded chambers, each communicating with the exterior by an inhalent pore (prosopyle).

A thicker or thinner specialized outer layer—the *dermal cortex*—situated immediately below the dermal epithelium, is present

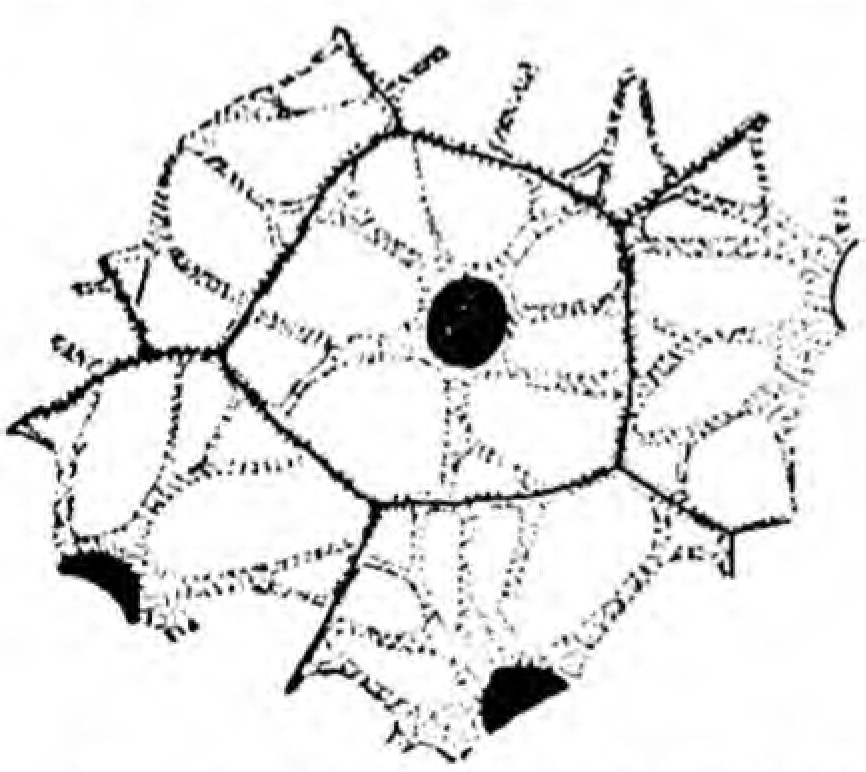


FIG. 92.—Cells of the dermal epithelium (pinacocytes) very highly magnified. (After Von Lendenfeld.)

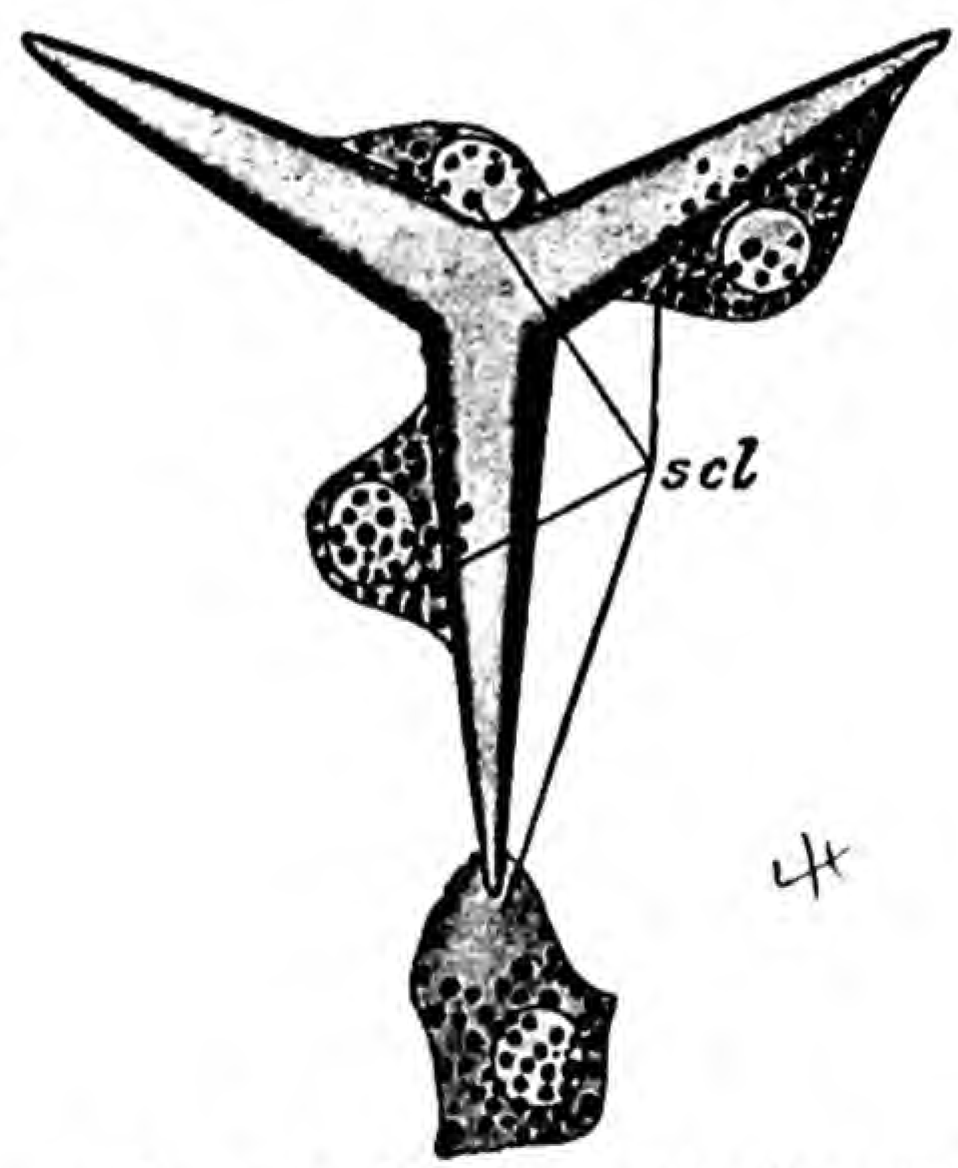


FIG. 93.—Development of a triradiate spicule of **Clathrina.** *scl.* scleroblasts. (After Minchin.)

in many Sponges. This is a layer with special skeletal elements, usually containing spaces and canals lined by dermal epithelium—(*subdermal cavities*, Fig. 91, *SD.*)—which communicate directly with the exterior, and, internally, usually with more deeply situated spaces (*subcortical cavities*), from which the incurrent canals lead to the ciliated chambers. This dermal cortex is present, though not highly developed, in Sycon gelatinosum (Fig. 85, *dc.*), and the enlarged outer ends of the incurrent canals lying in the dermal cortex and closed externally by the pore-bearing membrane may be regarded as representing dermal cavities. In most higher sponges a special inner layer is developed; this is the *gastral cortex*, represented in a rudimentary form in Sycon gelatinosum (Fig. 85, *gc.*) as the internal layer with special spicules, in which the excurrent canals are situated.

Histology.—In the protoplasmic elements or cells of the various groups of Sponges there is little variation, except in minor points. The cells (*pinacocytes*) of the dermal epithelium (Fig. 92) are flattened, and very rarely assume other forms; in some cases each flattened cell is provided with a flagellum. Lining the paragastric cavities and canals is a layer of flattened cells similar to those

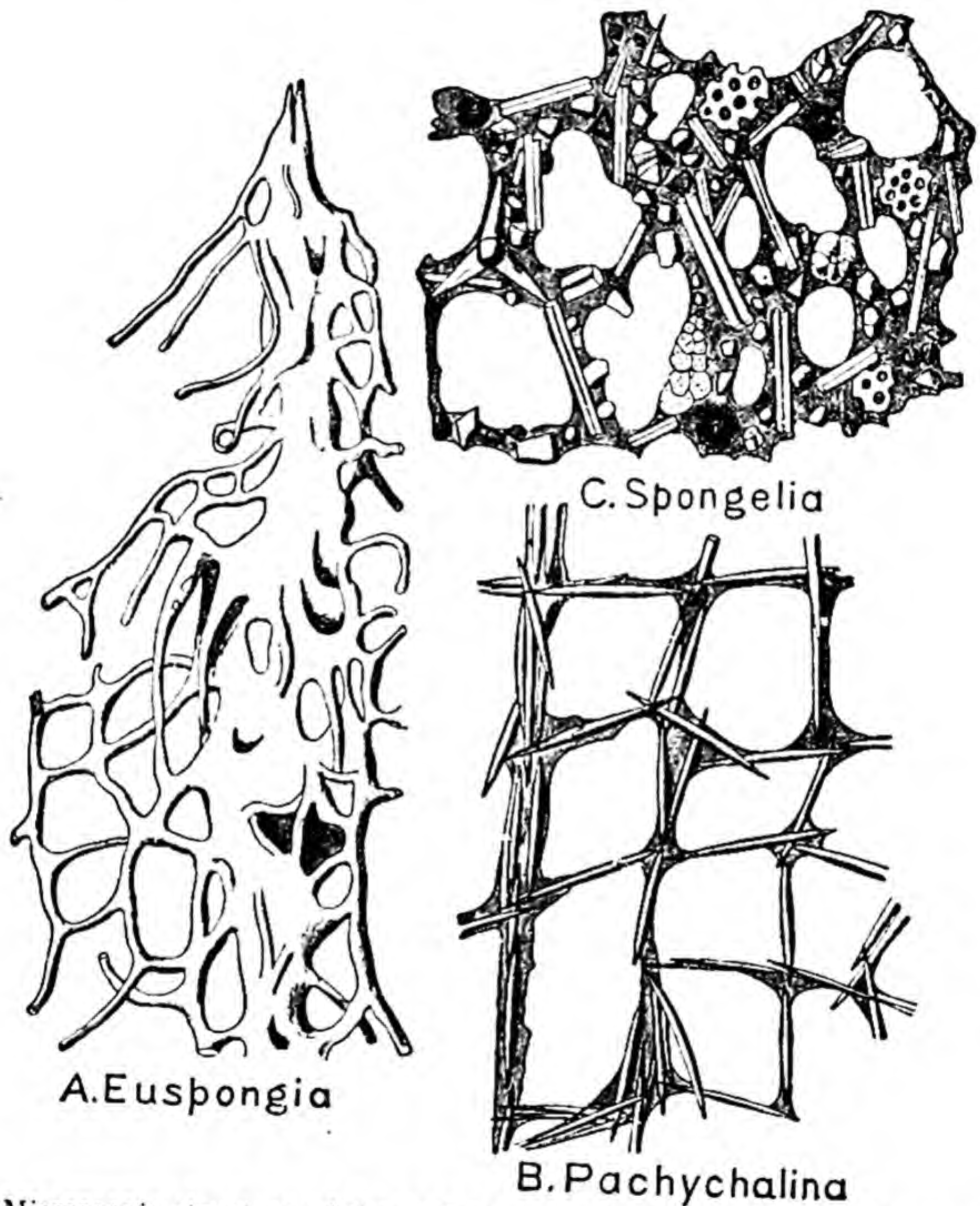


Fig. 94.—Microscopic structure of the skeleton in various sponges. *A*, **Euspongia,** network of spongin fibres; *B*, **Pachychalina,** spongin strengthened by siliceous spicules; *C*, **Spongelia,** spongin strengthened by various foreign siliceous bodies, fragments of spicules of other sponges, etc. (After Vosmaer.)

of the dermal epithelium, or of flagellate collared cells. In the gelatinous substance of the intermediate layer are embedded connective-tissue cells, amœboid wandering cells, and, in certain positions (around orifices), muscle-cells. Unicellular glands are present in some sponges, both calcareous and siliceous; also cells containing the pigment to which the bright colour of many sponges is due, though in most cases the pigment is not confined to special

cells, but occurs scattered through the connective-tissue cells and flagellate cells.

The elements of the **skeleton** differ in character in the different sub-classes and orders. In the Calcarea they consist of calcareous spicules, usually triradiate in form. Each of these spicules is developed from special cells—the *scleroblasts* (Fig. 93). In the remaining groups of Sponges the skeleton either consists of spongin fibres alone (Fig. 94, *A*), or of siliceous spicules alone, or of a combination of spongin fibres with siliceous spicules (*B*): in some Demospongia (the *Myxospongia*) skeletal parts are altogether absent. Spongin is a substance allied to silk in chemical composition and contains a large amount of iodine: the fibres are exceedingly fine threads, consisting of a soft granular core and an outer tube of concentric layers of spongin. These threads branch and anastomose, or are woven and felted together in such a way as to form a firm, elastic, supporting structure. They are secreted by the activity of certain cells in the gelatinous intermediate layer which are called the *spongoblasts*. In certain exceptional cases the spongin assumes the form of spicules. The siliceous spicules (Fig. 95) are much more varied in shape than the spicules of the Calcarea, and in a single kind of Sponge there may be a number of widely differing forms of spicules, each form having its special place in the skeleton of the various parts of the Sponge-body. In most forms siliceous spicules and spongin fibres combine to form the supporting framework, the relative development of these two elements varying greatly in different cases. But in certain groups, including the common washing-sponges (Fig. 94, *A*), spicules are completely absent, and the entire skeleton consists of spongin. In some forms which are devoid of spicules the place of these is taken by foreign bodies—shells of Radiolaria, grains of sand, or spicules from other sponges (Fig. 94, *C*). In others, again, such as the Venus's Flower-Basket (*Euplectella*), the Glass-Rope Sponge (*Hyalonema*), and *Pheronema* (Fig. 96), the skeleton consists throughout of siliceous spicules bound together by a siliceous cement.

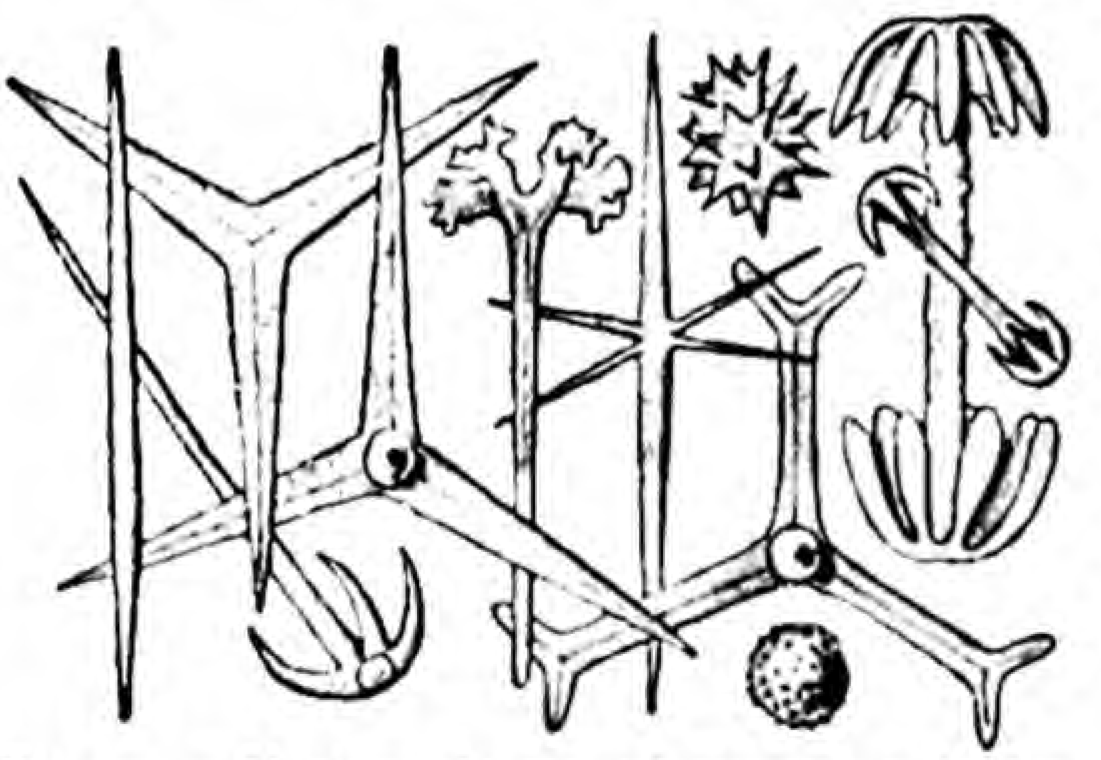


FIG. 95.—Various forms of sponge spicules. (From Lang's *Text-Book*.)

Reproduction in the Sponges is effected either sexually or asexually. In some cases asexual multiplication takes place by the production of external buds; in others of internal buds in the shape of groups of cells called *gemmules*, which eventually become detached and develop into new individuals. In the Fresh-water Sponges (*Spongillidæ*) multiplication takes place very actively by means of such gemmules, each of which is a spherical group of cells enclosed in an envelope often with peculiarly-shaped siliceous spicules, termed *amphi-*

discs (Fig. 95, right side). These gemmules are formed in the substance of the Sponge towards the end of the year; they are set free by the decay of the part of the parent sponge in which they are developed, and fall to the bottom. In

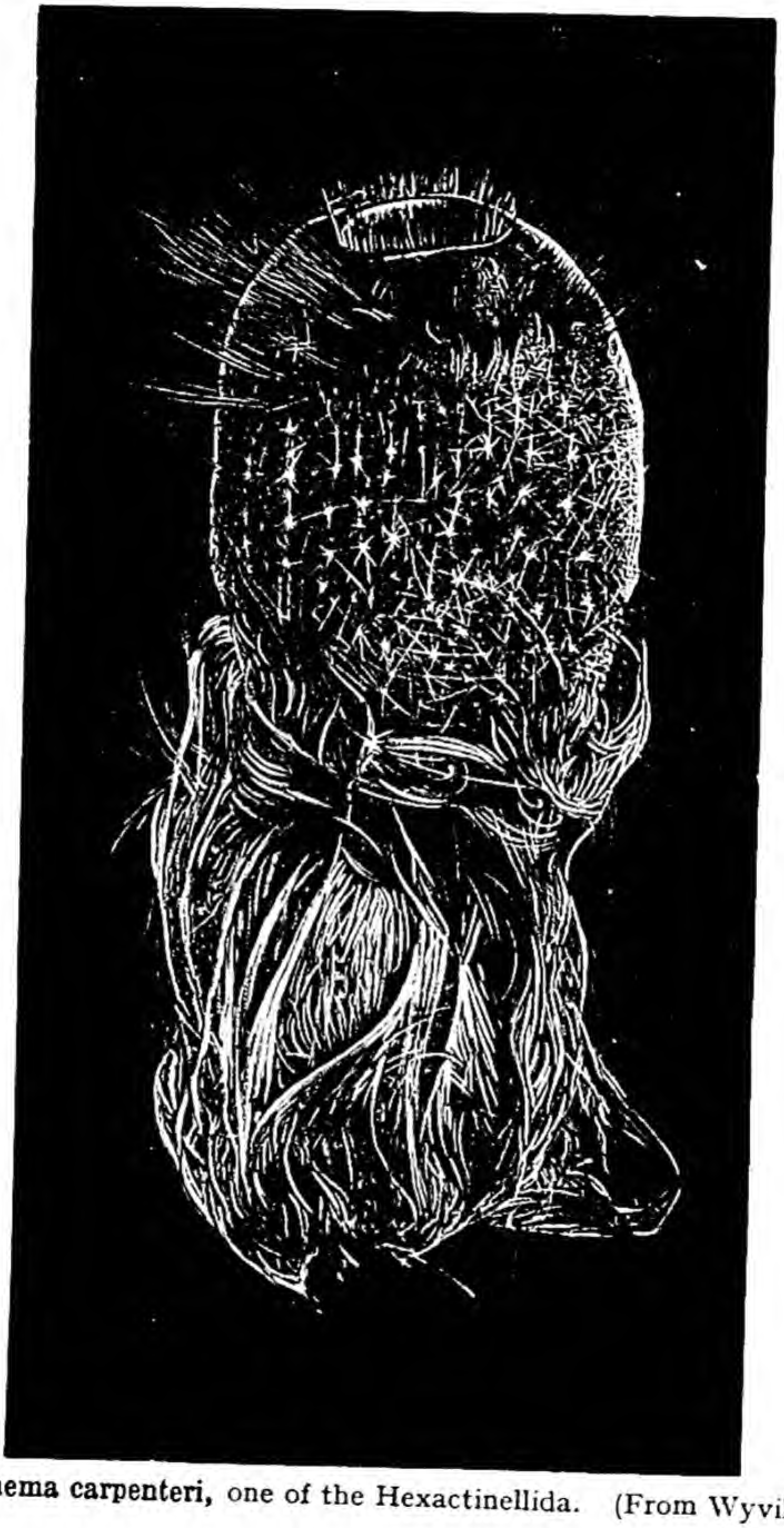


FIG. 96.—**Pheronema carpenteri,** one of the Hexactinellida. (From Wyville Thomson.)

spring the contained mass of protoplasmic matter reaches the exterior through an aperture in the wall of the gemmule, and develops into the adult form.

All Sponges multiply by a sexual process—by means of *sperms*, and *ova*.[1]

[1] Sexually-produced larvæ have not hitherto been found in the Hexactinellida or Tetractinellida.

These are developed from certain of the amœboid wandering cells, which take up a special position, usually immediately below the collared cells of the gastral epithelium. Ova and sperms are developed in the same Sponge, but rarely at the same time. The amœboid cell destined to form sperms divides into a number of small cells, giving rise to a rounded mass of sperms. The latter, when mature, have an oval or pear-shaped head and a long tapering appendage or tail. Each amœboid cell destined to form an ovum enlarges, and eventually assumes a spherical form. After a sperm has penetrated into its interior and effected fertilization, the ovum usually becomes enclosed in a brood-capsule formed for it by certain neighbouring cells, and in this situation, still enclosed in the parent Sponge, it undergoes the earlier stages of its development. The boring Sponge, *Cliona*, is the only one, so far as known, in which the early stages of development are passed through externally.

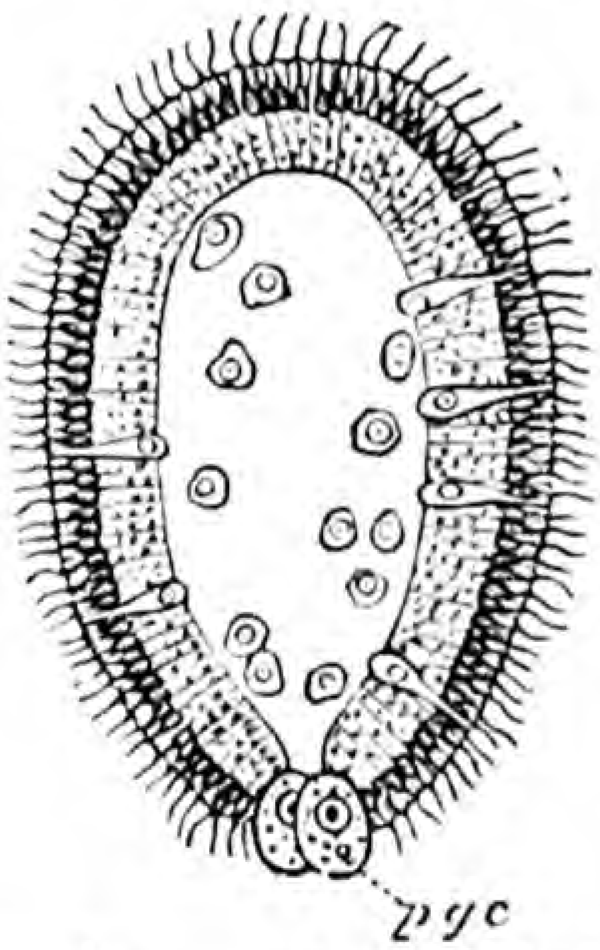


FIG. 97. — Median longitudinal section of the parenchymula larva of **Clathrina blanca.** *p. g. c.* posterior granular cells which give rise to the archæocytes. (From the Cambridge Natural History, after Minchin.)

In all known cases there is a free-swimming ciliated larval stage; but the form assumed by the larva differs profoundly in different Sponges. Of the simpler types of calcareous sponges with a structure resembling that of the *Olynthus*, the development has been followed out in the case of *Clathrina blanca*. In this sponge cleavage is followed by the formation of an oval blastula, the wall of which consists of a single layer of cells all alike in kind—elongated, columnar, and flagellate. At one pole of the blastula is seen a pair of cells which are of a different character, being large, rounded, and granular. These are destined to give rise to the *archæocytes*, some of which form the reproductive cells. Certain of the flagellate cells then withdraw their flagella and pass into the internal cavity, becoming amœboid. Soon a large number of these amœboid cells come to fill up a great part of the cavity of the larva, which now passes into a stage corresponding to the *planula* larva of the Cœlenterates (Section IV). This is the larval form known as the *parenchymula*. The parenchymula (Fig. 97) consists of three kinds of cells: (1) an external layer of flagellate cells; (2) an inner mass of amœboid cells; (3) the two posterior granular cells. In this condition it becomes fixed, and develops into the form of a flat plate with an irregular outline. Most of the amœboid cells now migrate to the outer surface, passing between the flagellate cells and then becoming arranged outside them to form the dermal epithelium. The flagellate cells now form an irregular mass together with a number of non-flagellate cells which are destined to give rise to the porocytes. A cavity appears in the mass, and becomes surrounded by a layer of porocytes. The cavity increases in size, and is soon seen to be bounded not

by the porocytes alone, but in part also by flagellate cells. Subsequently the flagellate cells come to form the entire boundary of the cavity, the porocytes passing outwards to become perforated by apertures—the inhalant apertures—in the wall of the sponge. Among the flagellate cells and porocytes there are also amœboid cells derived from the two original granular cells; some of these

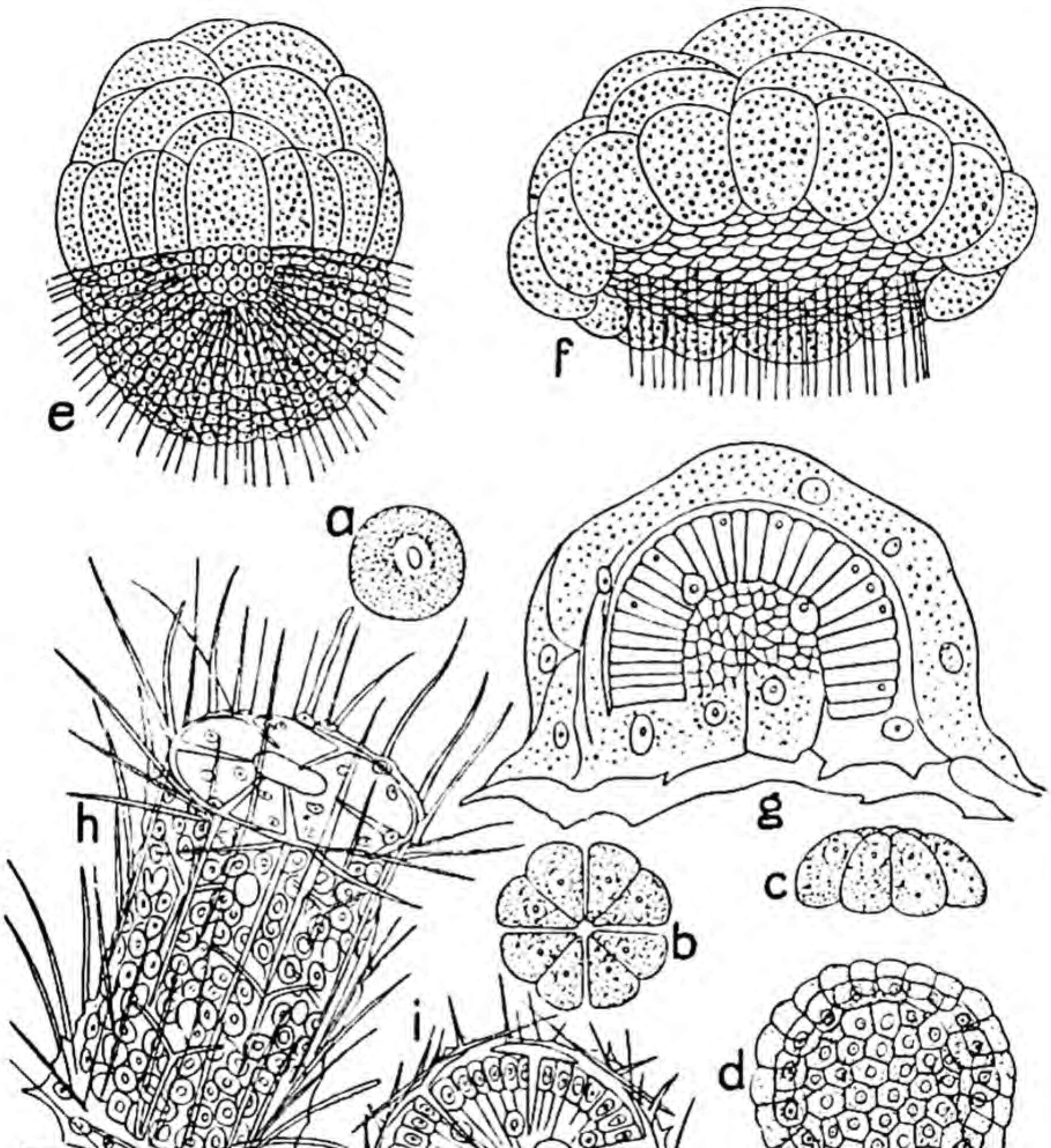


FIG. 98.—Development of **Sycon raphanus.** *a*, ovum; *b*, *c*, ovum cleaved—*b*, as seen from above, *c*, lateral view; *d*, blastula; *e*, amphiblastula; *f*, commencement of invagination; *g*, larva attached by its oral face; *h*, *i*, young sponge—*h*, lateral view; *i*, as seen from above. (From Sollas, after Schulze.)

give rise to the reproductive cells. The scleroblasts are formed of certain cells which migrate inwards, and at an early stage arrange themselves in three to give rise to the triradiate spicules. The development of the sponge becomes completed by the enlargement of the internal cavity (paragastric cavity) which is now lined by flagellate cells, and by the development of the osculum.

In *Sycon* the early stages (Fig. 98, *a–e*) differ somewhat from those in

Clathrina blanca, and the embryo leaves the parent sponge in the peculiar stage to which the name of *amphiblastula* is applied. When the blastula is formed the greater part of its wall consists of clear cells, with a number of granular cells—the archæocytes—at the posterior pole. The clear cells become elongated and flagellate. The archæocytes pass into the internal cavity and become completely enclosed by the flagellate cells (stage of so-called *pseudo-gastrula*).

The cells at the posterior end then lose their flagella and become large rounded granular cells, so that after a time the wall of the embryo comes to be composed in one half of the flagellate cells that have remained unaltered, and in the other half of the larger granular cells. It is in this stage—termed the *amphiblastula* (Fig. 98, *e*)—that the larval sponge becomes free. At a later stage the flagellate cells are partly overgrown by the granular cells, the latter eventually giving rise to the dermal epithelium of the adult, while the former become the flagellate collared cells. The larva fixes itself by one side, and soon assumes a cylindrical form (*h*, *i*). An aperture which is developed at the free end becomes the osculum, and small perforations in the sides of the cylinder form the inhalant apertures. As the wall of the cylinder increases in thickness by the growth of the intermediate layer, the radial canals are formed, the gastral layer extending into them, its cells remaining flagellate to form the choanocytes of the radial canals.

The amphiblastula type of larva is characteristic of the Calcarea, and is probably universal in that sub-class except in such primitive forms as *Clathrina*.

In the Silicispongiæ, on the other hand, the typical larva is a solid body with a superficial layer of flagellate cells, and an internal mass of granular cells. From the former, apparently, the collared cells of the flagellate chambers are formed: from the latter the external ectoderm and the other elements of the body of the Sponge. The granular cells break through the flagellate cells at one end and grow over the latter as an investing layer. This is a remarkable reversal of what, as will be seen subsequently, is to be observed in the Cœlenterata—and in fact in all Metazoa, but is readily reconcilable with what takes place in Sycon and the more complex Calcarea.

Distribution and Mode of Occurrence of Sponges and their Position in the Animal Series.—Fossil remains of Sponges have been found in various formations from those of the Cambrian period onwards, the greatest abundance being found in the Chalk. No extinct class or order has been detected, if we except the doubtfully-valid classes Octactinellida (Silurian only) and Heteractinellida (Carboniferous), the fossil forms all being members of existing groups.[1] Some of the orders of existing Sponges—such as the Myxospongiæ—are incapable of being preserved as fossils, and the fossil forms belong,

[1] The *Archæocyathinæ*, reef-forming organisms of Cambrian age, may have been nearly related to the Calcareous Sponges; but this remains doubtful.

as we should expect, to the more highly silicified groups and to the more complex groups of the Calcarea.

Freshwater Sponges (*Spongillidæ*) occur in rivers, canals, and lakes in all the great divisions of the earth's surface. Marine Sponges occur in all seas, and at all depths, from the shore between tide-marks to the deepest abysses of the ocean. The Calcarea and the true horny sponges (*Ceratosa*) are most abundant in shallow water, and have not been found below 450 fathoms. The Sponges found at the greatest depths are members of the groups *Hexactinellida* and *Choristida*.

Sponges do not appear to be edible by Fishes or even the higher Crustaceans or Molluscs. Countless lower animal forms, however, burrow in their substance, if not for food, at least for shelter, and the interior of a Sponge is frequently found to be teeming with small Crustaceans, Annelids, Molluscs, and other Invertebrates. None of the Sponges are true parasites. The little Boring Sponge, *Cliona*, burrows in the shells of Oysters and other bivalves, but for protection and not for food. But a Sponge frequently lives in that close association with another animal or plant to which the term *symbiosis or commensalism*, is applied, associations which benefit one or both. Thus some species of Sponge are never found growing except on the backs or legs of certain Crabs. In these cases the Sponge protects the Crab and conceals it from its enemies, while the Sponge benefits by being carried from place to place and thus obtaining freer oxygenation. Certain Cirripede Crustaceans (members of the order to which the Barnacles and Acorn-shells belong) are invariably found embedded in certain species of Sponge. Frequently a Sponge and a Zoophyte grow in intimate association, so that they seem almost to form one structure. Thus the Glass-rope Sponge (*Hyalonema*) is always found associated with a Zoophyte (*Palythoa*), and there are many other instances. Sponges often also grow in very close association with certain low forms of plants (Algæ).

The Porifera are unquestionably widely different from both Protozoa and Metazoa. The view that they are colonies of Protozoa is now no longer maintained, since the significance of the facts of their development has been fully recognized. Like the Metazoa, a sponge develops from a fertilized ovum by a process of cleavage. The sponges consist of a complex of cells, some of which have a considerable degree of independence, and some of which have a close resemblance to certain Protozoa; but the same is true of any one of the higher animals, the difference being one of degree and not of kind. Among the Protozoa the genus *Proterospongia* (Fig. 59, *4*), already referred to, appears to be the member of the latter group, which of all known forms most closely resembles a sponge. Proterospongia consists of a colony of collared Mastigophora (Choanoflagellata) embedded in a mass of gelatinous substance, in which there are also amœboid zooids similar to the amœboid wandering cells of sponges.

But while, for reasons dealt with above, the Porifera are to be separated from the Protozoa, there is some room for difference of opinion as regards their relationships to the *Cœlenterata*, with which great phylum they have been sometimes amalgamated. The reasons for the inclusion of the Porifera in a separate sub-kingdom will be discussed in considering the general relationships of the Cœlenterata (Section IV, p. 214).

SECTION IV

SUB-KINGDOM METAZOA

PHYLUM CŒLENTERATA

THE possession of an internal cavity lined by a special layer of cells—the endoderm—in which the digestive and absorptive functions are centred, distinguishes all the remaining groups of cellular animals from the Parazoa or Sponges. The former are grouped together under the comprehensive title of *Metazoa*. The simplest *Metazoa* have an internal cavity in which there is no separation between the enteric or digestive cavity and the general body-cavity—one continuous space (*cœlenteron*) representing both and opening on the exterior by the aperture of the mouth. These constitute the phylum *Cœlenterata*. They are all animals of a low type of organization with a conspicuous radial symmetry, disguising, in some cases, a more obscure bilateral arrangement, which may be more primitive.

The most familiar examples of Cœlenterata are the horny, seaweed-like "Zoophytes," to be picked up on every sea-beach—Jelly-fishes, Sea-anemones, and Corals. The phylum is subdivided as follows :—

SUB-PHYLUM CNIDARIA.

Class 1. HYDROZOA, including the Fresh-water Polypes, Zoophytes, many Jelly-fishes—mostly of small size—a few Stony Corals, and the peculiar Palæozoic fossils known as *Graptolites*.

Class 2. SCYPHOZOA, including most of the large Jelly-fishes.

Class 3. ACTINOZOA, including the Sea-anemones, and the vast majority of Stony Corals.

SUB-PHYLUM ACNIDARIA.

Class 1. CTENOPHORA, including certain peculiar Jelly-fishes known as "Comb-jellies."

SUB-PHYLUM CNIDARIA.

CLASS I.—HYDROZOA.

1. EXAMPLE OF THE CLASS—*Obelia*.

General Structure.—Obelia is a common zoophyte occurring in the form of a delicate, whitish or light brown, almost fur-like growth on seaweeds, the wooden

piles of piers, etc. It consists of branched filaments about the thickness of fine sewing-cotton: of these, some are closely adherent to the weed or timber, and serve for attachment, while others are given off at right angles, and present at intervals short lateral branches, each terminating in a bud-like enlargement.

The structure is better seen under a low power of the microscope. The organism (Fig. 99) is a colony, consisting of a common stem or axis, on which are borne numerous *zooids*. The axis consists of a horizontal portion (*hydrorhiza*) resembling a root or creeping stem, and of vertical axes, which give off short lateral branches in an alternate manner, bearing the zooids at their ends. At the proximal ends of the vertical axes the branching often becomes more complex: the offshoots of the main stem, instead of ending at once in a zooid, send off branches of the third order on which the zooids are borne. In many cases, also, branches are found to end in simple club-like dilatations (*Bd. 1, 2*): these are immature zooids.

The large majority of the zooids have the form of little conical structures (*P.1—P.4*), each enclosed in a glassy, cup-like investment or *hydrotheca* (*h.th.*), and produced distally into about two dozen arms or *tentacles* (*t.*): these zooids are the *polypes* or *hydranths*. Less numerous, and found chiefly towards the proximal region of the colony, are long cylindrical bodies or *blastostyles* (*bls.*), each enclosed in a transparent case, the *gonotheca* (*g.th.*), and bearing numerous small lateral offshoots, varying greatly in form according to their stage of development, and known as *medusa-buds* (*m.bd.*). By studying the development of these structures, and by a comparison with other forms, it is known that both blastostyles and medusa-buds are zooids, so that the colony is *trimorphic*, having zooids of three kinds.

To make out the structure in greater detail, living specimens should be observed under a high power. A polype is then seen to consist of a somewhat cylindrical, hollow *body*, of a yellowish colour, joined to the common stem by its proximal end, and produced at its distal end into a conical elevation, the *manubrium* or *oral cone* (*mnb.*), around the base of which are arranged the twenty-four tentacles in a circle. Both body and manubrium are hollow, containing a spacious cavity, the *cœlenteron* (*ent.*), which communicates with the outer world by the *mouth* (*mth.*), an aperture placed at the summit of the manubrium. The mouth is capable of great dilatation and contraction, and accordingly the manubrium appears now conical, now trumpet-shaped. Under favourable circumstances small organisms may be seen to be caught by the polypes and carried towards the mouth to be swallowed.

The hydrotheca (*h.th.*) has the form of a vase or wine-glass, and is perfectly transparent and colourless. A short distance from its narrow or proximal end, it is produced inwards into a sort of circular shelf (*sh.*), perforated in the centre: upon this the base of the polype rests, and through the aperture it is continuous with the common stem. When irritated—by a touch or by the addition

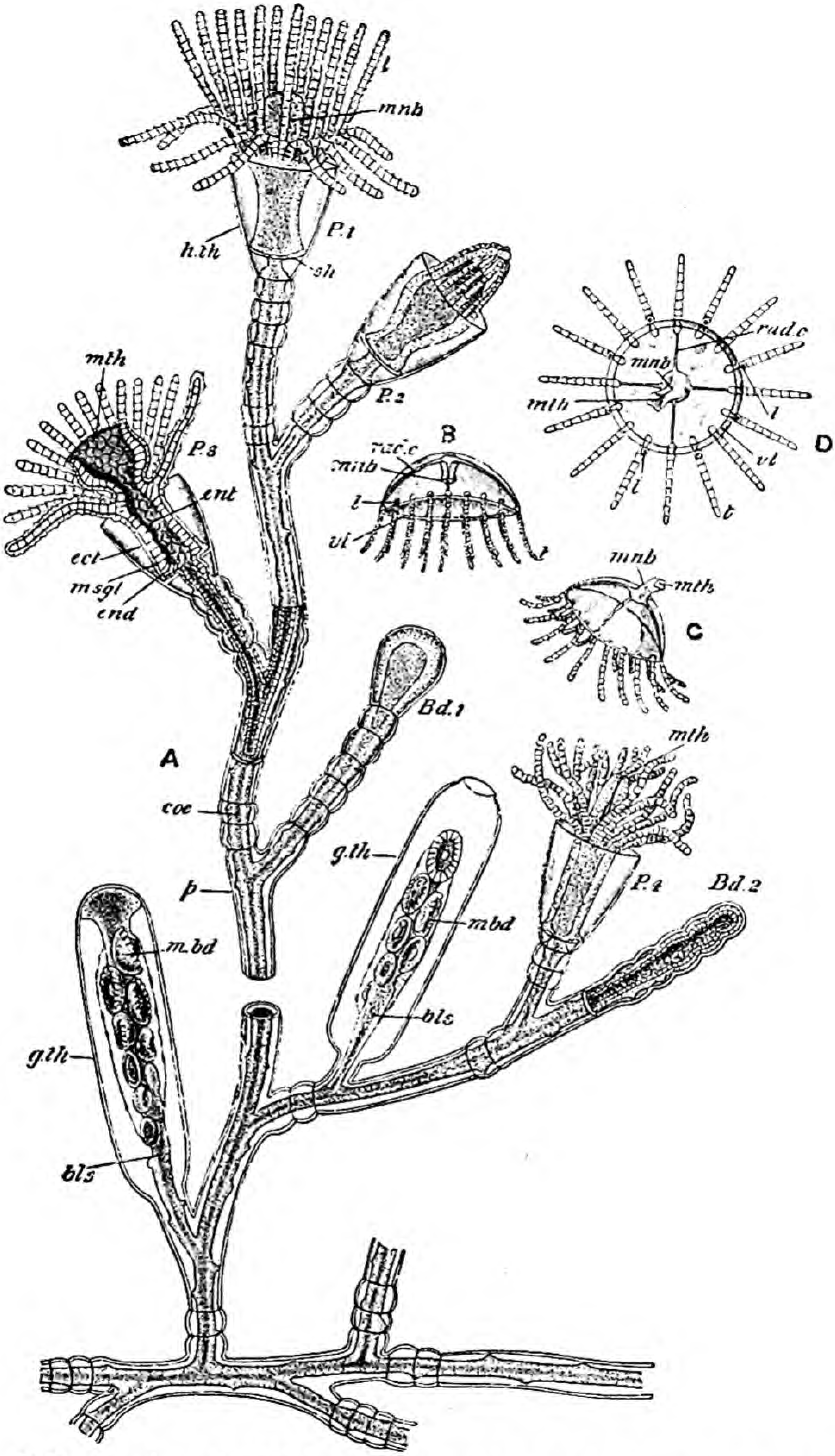


FIG. 99.—**Obelia sp.** *A*, portion of a colony with certain parts shown in longitudinal section; *B*, medusa; *C*, the same with reversed umbrella; *D*, the same, oral aspect; *Bd. 1, 2*, buds; *bls.* blastostyle; *cœ.* cœnosarc; *ect.* ectoderm; *end.* endoderm; *ent.* enteric cavity (*cœlenteron*); *g.th.* gonotheca; *h.th.* hydrotheca; *l.* lithocyst; *m.bd.* medusa-bud; *mnb.* manubrium; *msgl.* mesoglœa; *mth.* mouth; *p.* perisarc; *P. 1, 2, 3,* polypes; *rad. c.* radial canal; *t.* tentacle; *vl.* velum.

of an irritating chemical substance—the polype undergoes a very marked contraction: it suddenly withdraws itself more or less completely into the theca, and the tentacles become greatly shortened and curved over the manubrium (*P. 2*).

The various branches of the common stem show a very obvious distinction into two layers: a transparent, tough, outer membrane, of a yellowish colour and horny consistency, the *perisarc* (*p.*), and an inner, delicate, granular layer, the *cœnosarc* (*cœ.*), continuous by a sort of neck or constriction with the body of each hydranth. The cœnosarc is hollow, its tubular cavity being continuous with the cavities of the polypes, and containing a fluid in which a flickering movement may be observed, due, as we shall see, to the action of cilia. At the base of each zooid or branch the perisarc presents several annular constrictions, giving it a ringed appearance: for the most part it is separated by an interval from the cœnosarc, but processes of the latter extend outwards to it at irregular intervals, and in the undeveloped zooids (*Bd. 2*) the two layers are in close apposition.

In the blastostyle both mouth and tentacles are absent, the zooid ending distally in a flattened disc: the hydrotheca of a polype is represented by the gonotheca (*g.th.*), which is a cylindrical capsule enclosing the whole structure, but ultimately becoming ruptured at its distal end to allow of the escape of the medusa-buds. These latter are, in the young condition, mere hollow offshoots of the blastostyle: when fully developed they have the appearance of saucers attached by the middle of the convex surface to the blastostyle, produced at the edge into sixteen very short tentacles, and having a blunt process, the manubrium, projecting from the centre of the concave surface. They are ultimately set free through the aperture in the gonotheca as little *medusæ* or jelly-fish (*B—D*), which will be described hereafter.

The **microscopical structure** of a polype (Fig. 100) reminds us, in its general features, of that of such a simple sponge as Ascetta, but with many characteristic differences. The body is composed of two layers of cells, the ectoderm (*ect.*) and the endoderm (*end.*): between them is a very delicate transparent membrane, the *mesoglœa* or *supporting lamella* (*msgl.*), which, unlike the intermediate layer of sponges, contains no cells and is practically structureless. The same three layers occur in the manubrium, the ectoderm and endoderm being continuous with one another at the margin of the mouth. The tentacles are formed of an outer layer of ectoderm, then a layer of mesoglœa, and finally a solid core of large endoderm cells arranged in a single series. The cœnosarc, blastostyles, and medusa-buds all consist of the same layers, which are thus continuous through the entire colony.

The perisarc or transparent outer layer of the stem shows no cell-structure, but only a delicate lamination. It is, in fact, not a cellular membrane or epithelium, like the ectoderm and endoderm, but a *cuticle*, formed, layer by

layer, as a secretion from the ectoderm cells. It is composed of a substance of chitinoid or horn-like consistency, and, like the lorica of many Protozoa, serves as a protective external skeleton. When first formed it is of course in contact with the ectoderm, but when the full thickness is attained the latter retreats from it, the connection being maintained only at irregular intervals. In the same way the hydro- and gonothecæ are cuticular products of the polypes and blastostyles respectively: in the young condition both occur in the form of a closely fitting investment of the knob-like rudiment of the zooid (Fig. 99, *Bd. 1, 2*).

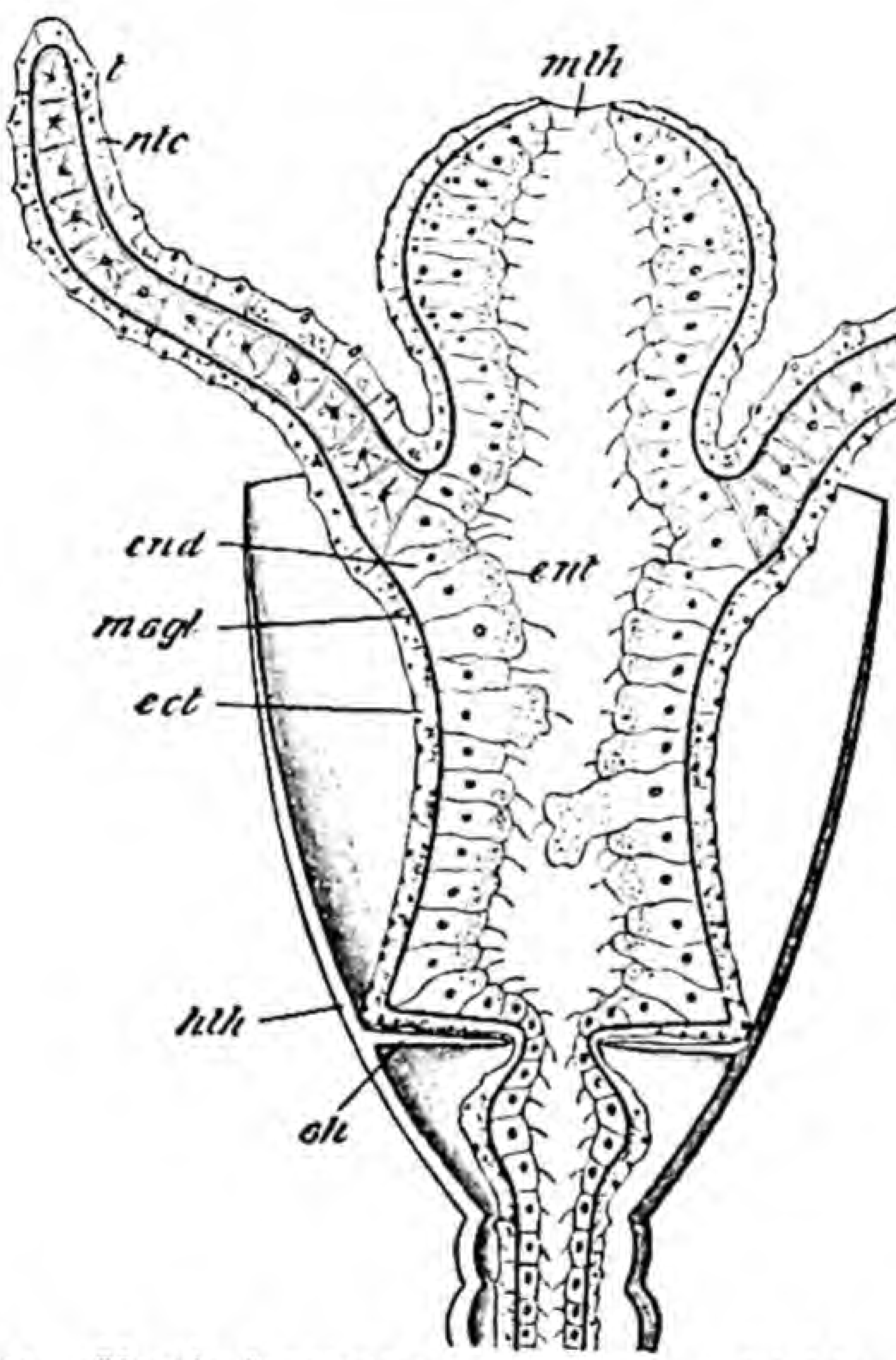


FIG. 100.—**Obelia sp.** Vertical section of a polype, highly magnified; *ect.* ectoderm; *end.* endoderm; *ent.* enteric cavity (*cœlenteron*); *h.th.* hydrotheca; *msgl.* mesoglœa; *mth.* mouth; *ntc.* nematocysts; *sh.* shelf-like prolongation of hydrotheca; *t.* tentacle.

The ectoderm has the general character of a columnar epithelium, but exhibits considerable differentiation of its component cells. It is mainly composed of large conical cells with their bases outwards, and having between their narrow inner ends clumps of small rounded *interstitial cells*, and occasional large branched *nerve-cells* (Fig. 101, *nv.c.*). The tentacles and the manubrium contain, in addition, a layer of unstriped *muscle-fibres* between the ectoderm and the mesoglœa: they are arranged longitudinally, and serve for the rapid shortening of the tentacles.

Embedded in the ectoderm are numerous clear ovoid bodies, the *stinging-capsules* or *nematocysts* (Figs. 100 and 101, *ntc.*), organs closely resembling those of the protozoon *Epistylis umbellaria*, and, like them, serving as weapons of

offence. Each consists (Fig. 101, *A*) of a tough ovoid capsule, full of fluid, and invaginated at one end in the form of a hollow process continued into a long, coiled, hollow thread. The whole apparatus is developed from an interstitial cell forming a *cnidoblast* (*cnb.*), which, as it approaches maturity, migrates to the surface where it becomes part of the ectodermal epithelium. At one point of its surface the cnidoblast is produced into a delicate protoplasmic process, the *cnidocil* or *trigger-hair* (*cnc.*) : when this is touched—for

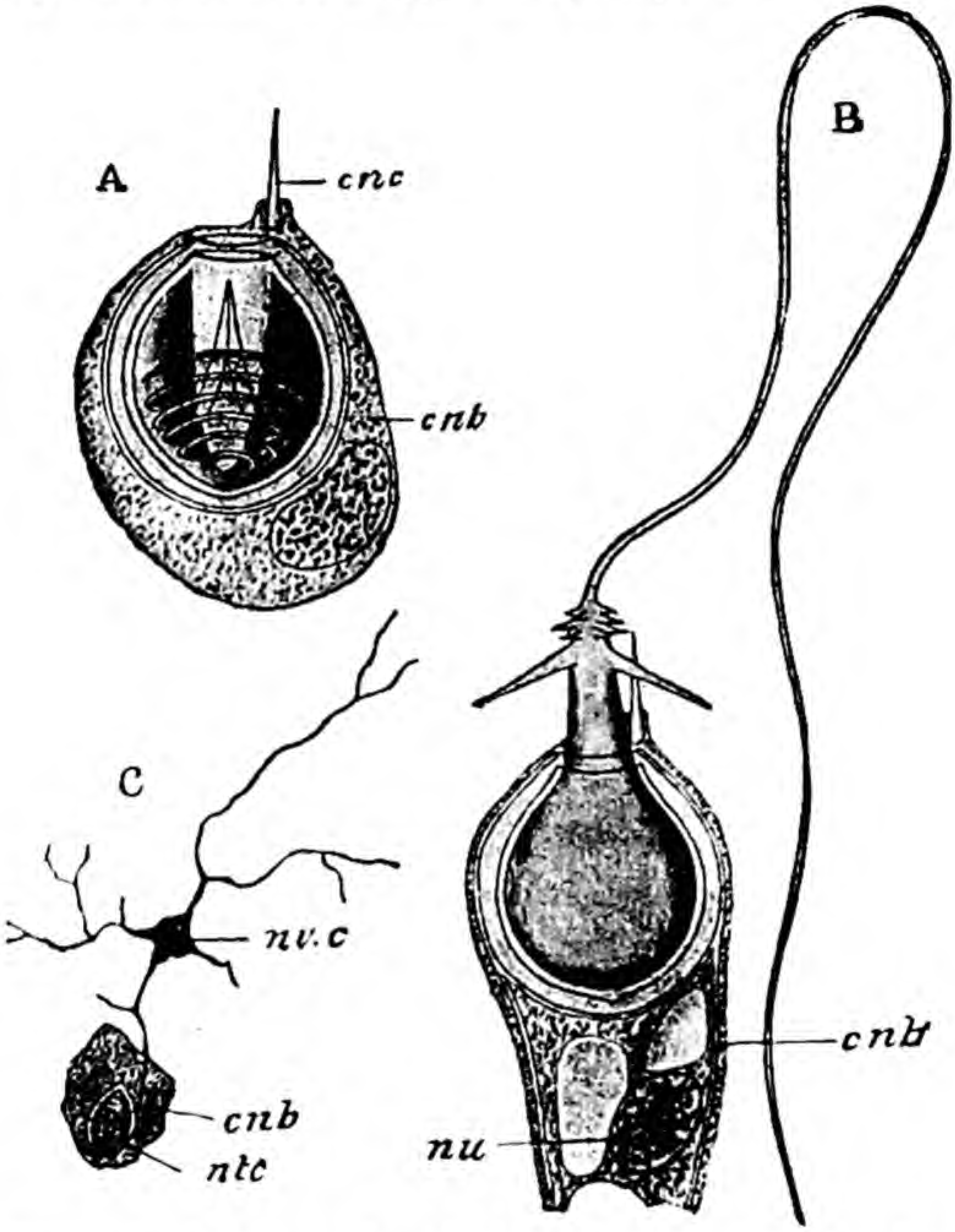


FIG. 101.—Nematocysts of **Hydra.** *A*, undischarged ; *B*, discharged ; *C*, nerve-supply ; *cnb.* cnidoblast ; *cnc.* cnidocil ; *nu.* nucleus ; *ntc.* nematocyst ; *nv.c.* nerve-cell. (From Parker's *Biology*, after Schneider.)

instance by some small organism brought into contact with the waving tentacle —the cnidoblast undergoes a sudden contraction, and the pressure upon the stinging capsule causes an instantaneous eversion of the thread (*B*), at the base of which are minute barbs. The threads are poisonous, and exert a numbing effect on the animals upon which Obelia preys.

The endoderm also has the general character of a columnar epithelium. In the body of the polype the cells are very large and have the power of sending

out pseudopods at their free ends (Fig. 100), which apparently seize and ingest minute portions of the partly-digested food. As in many Protozoa, the pseudopods may be drawn in and long flagella protruded, the contraction of which causes a constant movement of the food particles in the enteric cavity. Amongst these large cells are narrow cells with very granular protoplasm: they are gland-cells, and secrete a digestive juice. In the manubrium a layer of muscle-fibres has been described taking a transverse direction, and so serving to antagonize the longitudinal muscles and contract the cavity. In the tentacles (Fig. 100) the endoderm (*end.*) consists of a single row of short cylindrical cells, nearly cubical in longitudinal section: their protoplasm is greatly vacuolated and their cell-walls are so thick that they may be considered as forming a sort of internal skeleton to the tentacles.

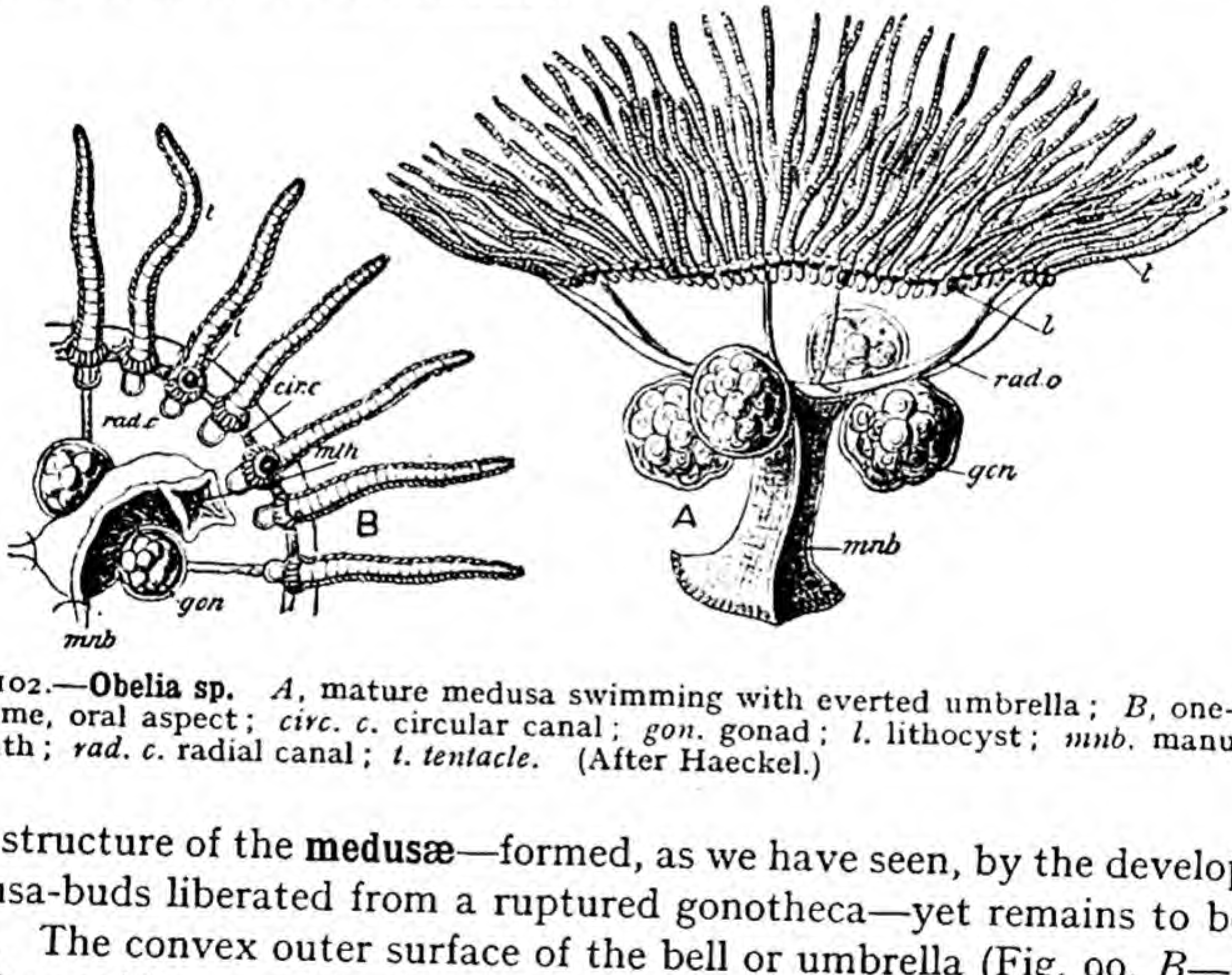


FIG. 102.—**Obelia sp.** *A*, mature medusa swimming with everted umbrella; *B*, one-quarter of the same, oral aspect; *circ. c.* circular canal; *gon.* gonad; *l.* lithocyst; *mnb.* manubrium; *mth.* mouth; *rad. c.* radial canal; *t. tentacle.* (After Haeckel.)

The structure of the **medusæ**—formed, as we have seen, by the development of medusa-buds liberated from a ruptured gonotheca—yet remains to be considered. The convex outer surface of the bell or umbrella (Fig. 99, *B*—*D*) by which the zooid was originally attached to the blastostyle is distinguished as the *ex-umbrella*, the concave inner surface as the *sub-umbrella*. From the centre of the sub-umbrella proceeds the manubrium (*mnb.*), at the free end of which is the four-sided mouth (*mth.*). Very commonly, as the medusa swims the umbrella becomes turned inside out, the sub-umbrella then forming the convex surface and the manubrium springing from its apex (Fig. 99, *C*, and Fig. 102, *A*).

The mouth (Figs. 99, 100, 102, and 103, *mth.*) leads into an enteric cavity which occupies the whole interior of the manubrium, and from its dilated base sends off four delicate tubes, the *radial canals* (*rad. c.*), which pass at equal distances from each other through the substance of the umbrella to its margin,

where they all open into a *circular canal* (*circ. c.*), running parallel with and close to the margin. By means of this system of canals the food, taken in at the mouth and digested in the manubrium, is distributed to the entire medusa.

The edge of the umbrella is produced into a very narrow fold or shelf, the *velum* (Fig. 103, *vl.*), and gives off the tentacles (*t.*), which are sixteen in number in the newly-born medusa (Fig. 99), very numerous in the adult (Fig. 102). At the bases of eight of the tentacles—two in each quadrant—are minute globular sacs (*l.*), each containing a calcareous body in contact with hair-like processes of sensory cells. These are the *marginal sense-organs* or *lithocysts.* They are organs concerned in the co-ordination of swimming movements.

The manubrium (Fig. 103, *mnb.*) of the medusa consists of precisely the same layers as that of the hydranth—ectoderm, mesoglœa, and endoderm. The ecto-

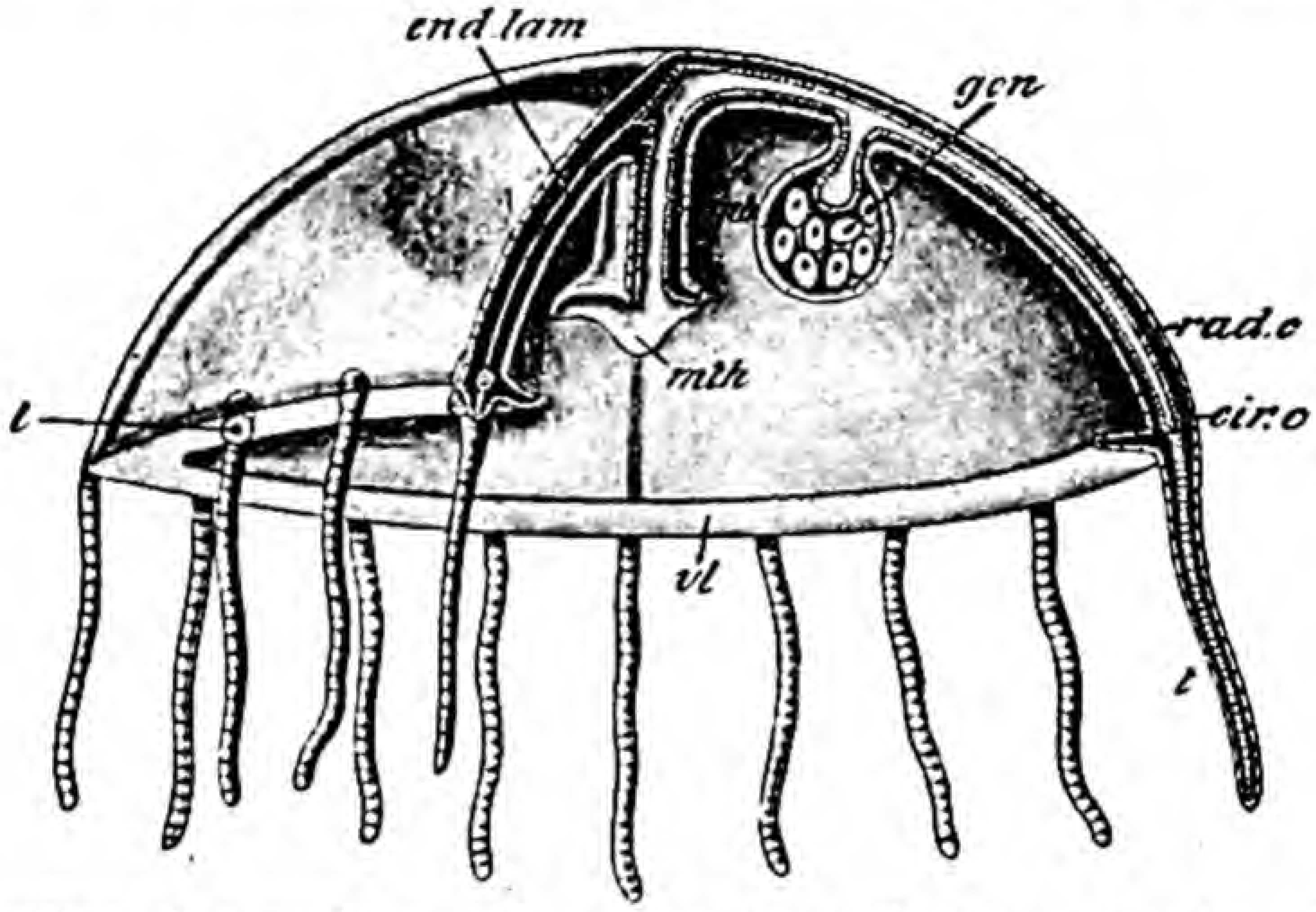


FIG. 103.—Dissection of a **medusa** with rather more than one-quarter of the umbrella and manubrium cut away (diagrammatic). The ectoderm is dotted, the endoderm striated, and the mesoglœa black; *circ. c.* circular canal; *end. lam.* endoderm lamella; *gon.* gonad; *l.* lit hocyst; *mnb.* manubrium; *mth.* mouth; *rad. c.* radial canal; *vl.* velum.

derm is continued on to the sub-umbrella, and then round the margin of the bell on to the ex-umbrella, so that both surfaces of the bell are covered with ectoderm. The endoderm is continued from the base of the enteric cavity into the radial canals and thence to the circular canal, so that the whole canal-system is lined by endoderm. In the portions of the bell between the radial canals there is found, between the outer and inner layers of ectoderm, a thin sheet of endoderm, the *endoderm-lamella* (*end.lam.*), which stretches between adjacent radial canals and between the circular canal and the enteric cavity. In the bell, as in the manubrium, a layer of mesoglœa everywhere intervenes between ectoderm and endoderm.

The velum (*vl.*) consists of a double layer of ectoderm and a middle one of mesoglœa: there is no extension of endoderm into it. The tentacles, like those of the hydranth, are formed of a core of endoderm covered by ectoderm, the cells of the latter being abundantly supplied with stinging-capsules.

Comparison of Polype and Medusa.—Striking as is the difference between a polype and a medusa, they are strictly homologous structures, and the more complex medusa is readily derivable from the simpler polype-form. It is

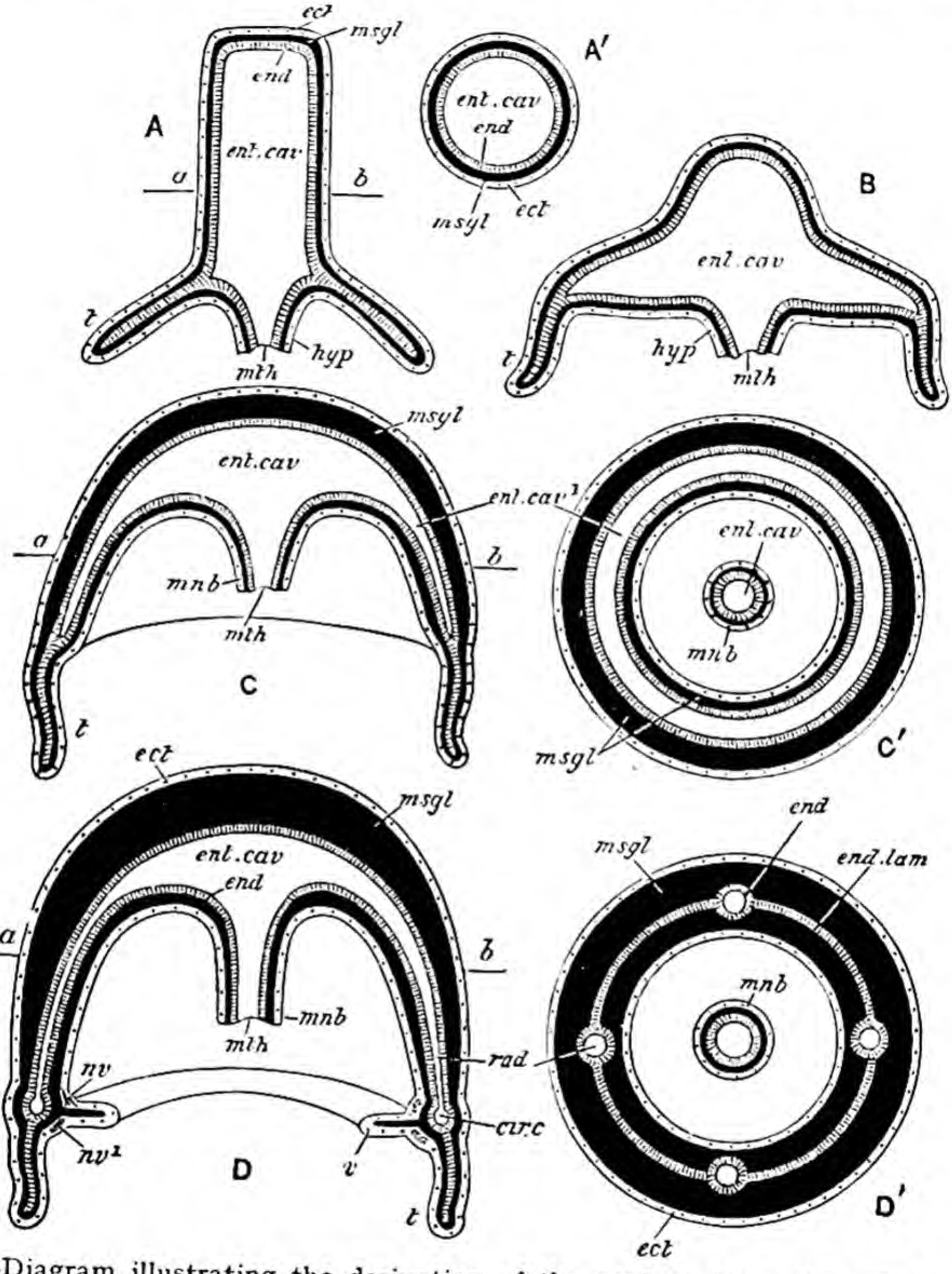


FIG. 104.—Diagram illustrating the derivation of the **medusa** from the **polype.** *A*, longitudinal, and *A′*, transverse section (along the line *ab*) of polype-form; *B*, polype-form with extended tentacular region; *C*, vertical, and *C′*, transverse section (along the line *ab*) of form with tentacular region extended into the form of a bell; *D*, vertical, and *D′*, transverse section (along the line *ab*) of medusa. The ectoderm is dotted, the endoderm striated, and the mesoglœa black. *cir. c.* circular canal; *ect.* ectoderm; *end.* endoderm; *end. lam.* endoderm lamella; *ent. cav.* enteric cavity; *hyp.* hypostome or manubrium; *mnb.* manubrium; *msgl.* mesoglœa; *mth.* mouth; *nv.*, *nv′*. nerve-rings; *t.* tentacle; *v.* velum. (From Parker's *Biology*.)

obvious, in the first instance, that the apex of the umbrella corresponds with the base of a hydranth (Fig. 104, *A* and *D*), being the part by which the zooid is attached in each case to the parent stem: the mouth with the manubrium are also obviously homologous structures in the two cases. Suppose the tentacular

region of a polype to be pulled out, as it were, into a disc-like form (*B*), and afterwards to be bent into the form of a saucer (*C*) with the concavity distal, *i.e.*, towards the manubrium. The result of this would be a medusa-like body (*C*, *C'*) with a double wall to the entire bell, the narrow space between the two layers containing a prolongation of the cœlenteron (*ent. cav'.*) and being lined with

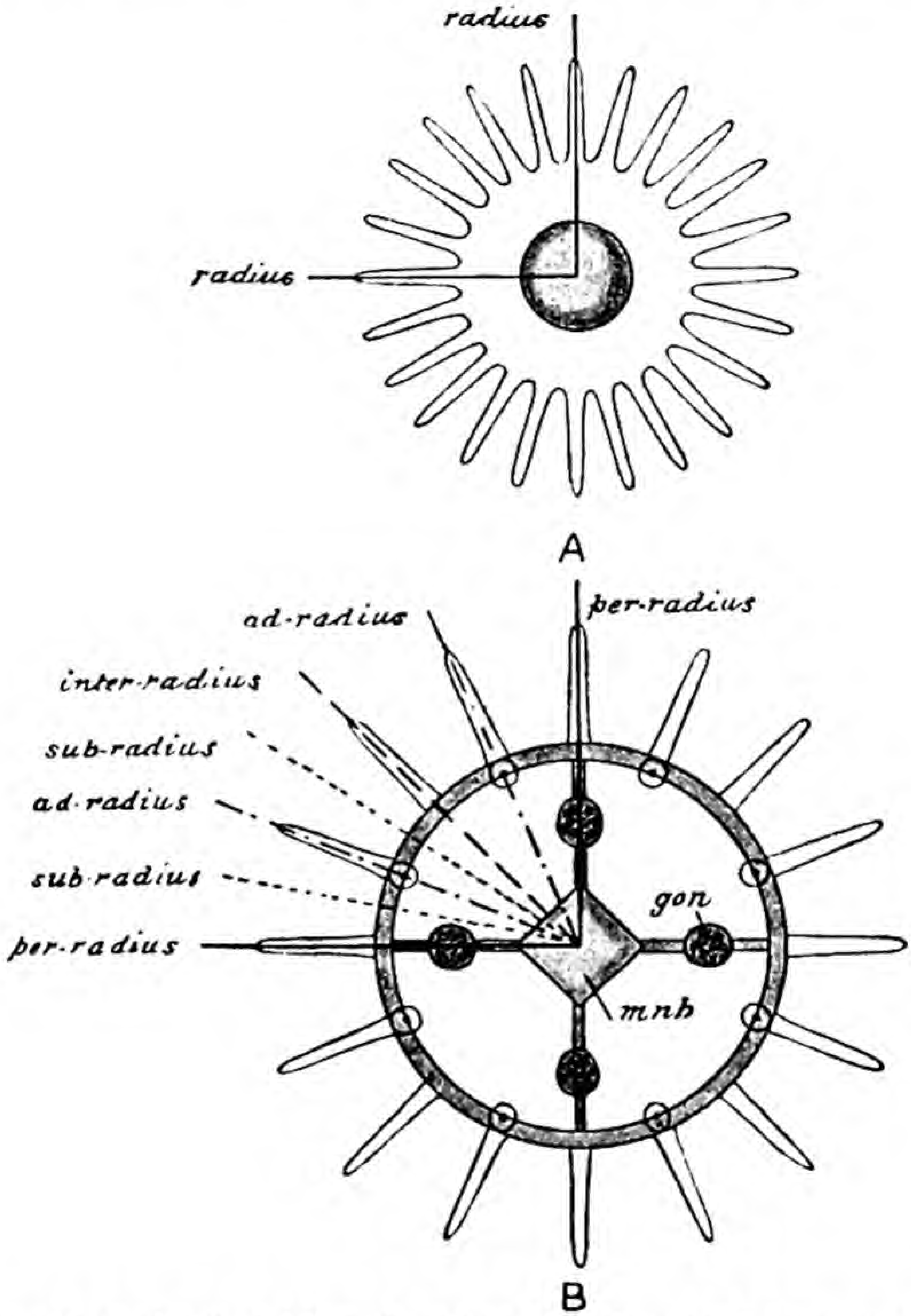


FIG. 105.—Projections of **polype** (*A*) and **medusa** (*B*), showing the various orders of radii *gon.* gonad; *mnb.* manubrium.

endoderm. From such a form the actual condition of things found in the medusa would be produced by the continuous cavity in the bell being for the most part obliterated by the growing together of its walls so as to form the endoderm-lamella (*D'*, *end. lam.*), and remaining only along four meridional areas—the radial canals (*rad. c.*), and a circular area close to the edge of the bell—the circular canal (*cir. c.*).

While both polype and medusa are radially symmetrical, the increase in complexity of the medusa is accompanied by a differentiation of the structures lying along certain radii. If a polype is projected on a plane surface (Fig. 105, *A*), taken at right angles to its long axis, a large number of radii—about twenty-four—can be drawn from the centre outwards, all passing through similar parts, *i.e.*, along the axis of a tentacle and through similar portions of the body and manubrium. But in the medusa (*B*) the case is different. The presence of the four radial canals allows us to distinguish four *principal radii* or *per-radii*. Halfway between any two per-radii a *radius of the second order*, or *inter-radius* may be taken; halfway between any per-radius and the inter-radius on either side a *radius of the third order*, or *ad-radius*, and halfway between any ad-radius and the adjacent per- or inter-radius, a *radius of the fourth order*, or *sub-radius*. Thus there are four per-radii, four inter-radii, eight ad-radii, and sixteen sub-radii. In Obelia the radial canals, the angles of the mouth, and four of the tentacles are per-radial, four more tentacles are inter-radial, and the remaining eight tentacles, bearing the lithocysts, are ad-radial. The sub-radii are of no importance in this particular form.

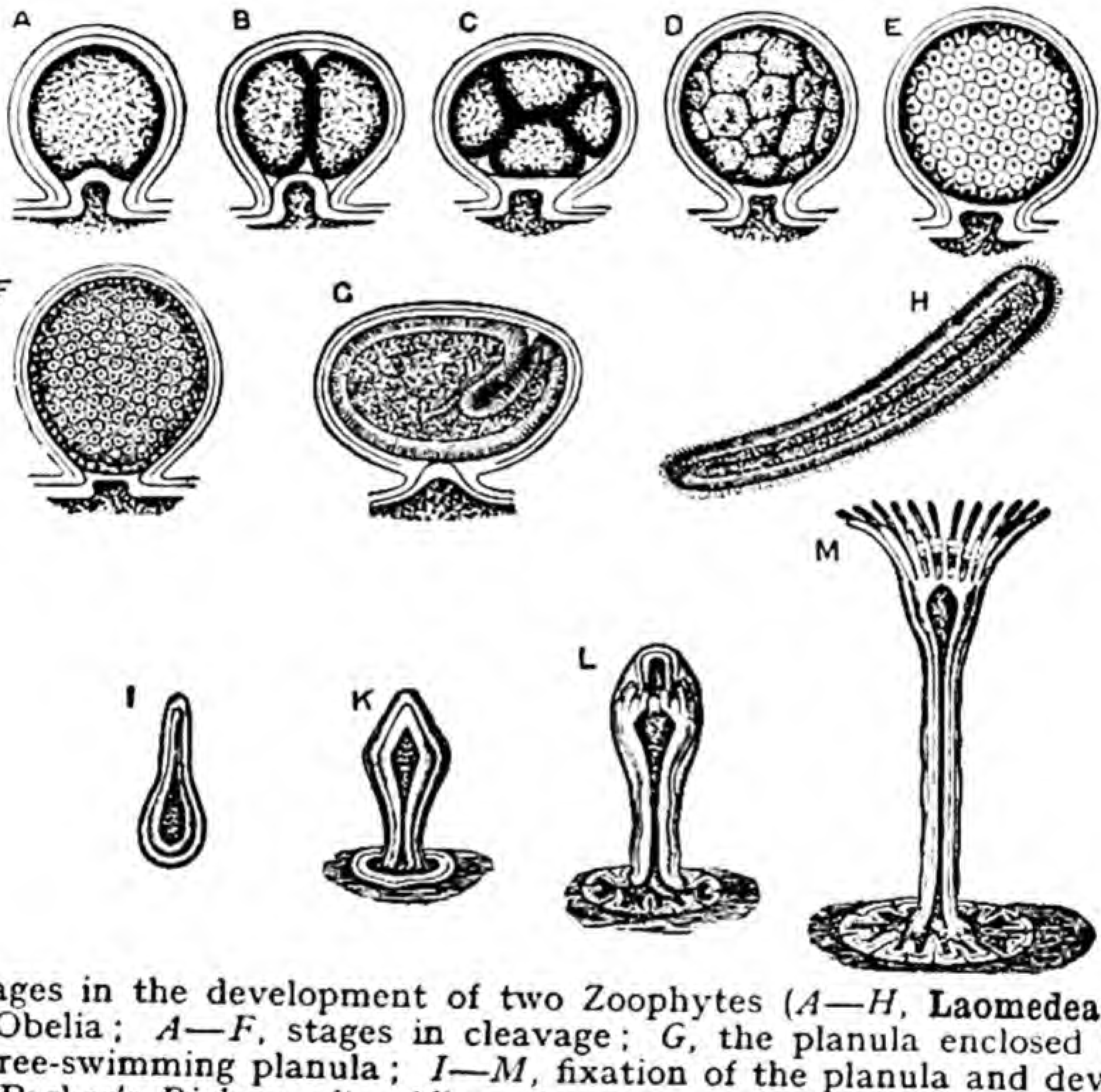


FIG. 106.—Stages in the development of two Zoophytes (*A—H*, **Laomedea**, *I—M*, **Eudendrium**) allied to Obelia; *A—F*, stages in cleavage; *G*, the planula enclosed in the maternal tissues; *H*, the free-swimming planula; *I—M*, fixation of the planula and development of the hydrula. (From Parker's *Biology*, after Allman.)

Reproduction.—In the description of the fixed Obelia-colony no mention was made of cells set apart for reproduction, like the ova and sperms of a sponge. As a matter of fact, such sexual cells are found only—in their fully developed condition at least—in the medusæ. Hanging at equal distances from the sub-umbrella, in immediate relation with the radial canal and therefore per-radial in position, are four ovoid bodies (Figs. 102 and 103, *gon.*), each consisting of an outer layer of ectoderm continuous with that of the sub-umbrella, an inner layer of endoderm continuous with that of the radial canal and enclosing a prolongation of the latter, and of an intermediate mass of cells which have become differentiated into ova or sperms. As each medusa bears organs of one sex only (testes or ovaries, as the case may be), the individual medusæ

are *diœcious*. It will be noticed that the gonad has the same general structure as an immature zooid—an outpushing of the body-wall consisting of ectoderm and endoderm, and containing a prolongation of the enteric cavity.

Development.—When the gonads are ripe, the sperms of the male medusæ are shed into the water and carried by currents to the females fertilizing the ova. The zygote undergoes complete cleavage (Fig. 106, *A—F*), and is converted into an ovoidal body called a *planula* (*G, H*), consisting of an outer layer of ciliated ectoderm cells and an inner mass of endoderm cells in which a space appears, the rudiment of the cœlenteron. The planula swims freely for a time (*H*), then settles down on a piece of timber, seaweed, etc., fixes itself by one end (*K*), and becomes converted into a *hydrula* or simple polype (*L, M*), having a disc of attachment at its proximal end, and at its distal end a manubrium and circlet of tentacles. Soon the hydrula sends out lateral buds, and, by a frequent repetition of this process, becomes converted into the complex Obelia-colony with which we started.

This remarkable life-history furnishes the first example we have yet met with among the Metazoa of *alternation of generations*, or *metagenesis*. The Obelia-colony is sexless, having no gonads, and developing only by the asexual process of budding; but certain of its buds—the medusæ—develop gonads, and from their fertilized eggs new Obelia-colonies arise. We thus have an alternation of an *asexual generation*—the Obelia-colony, with a *sexual generation*—the medusa.

2. Distinctive Characters and Classification.

The Hydrozoa may be defined as multicellular animals in which the cells are arranged in two layers, ectoderm and endoderm, separated by a gelatinous mesoglœa, and enclosing a continuous digestive cavity which communicates directly with the exterior by a single aperture—the mouth—and is lined throughout by endoderm. The ectoderm consists of epithelial cells, interstitial cells, muscle-fibres, and nerve-cells. Certain of the interstitial cells give rise to characteristic organs of offence—the stinging-capsules. The endoderm consists of flagellate or amœboid cells, gland-cells, and sometimes muscle-fibres. There are two main forms of zooids, polypes or nutritive zooids, which are usually sexless, and medusæ or reproductive zooids. In correspondence with its locomotive habits, the medusa attains a higher degree of organization than the polype, having more perfect muscular and nervous systems, distinct sense-organs, and a digestive cavity differentiated into central and peripheral portions, the latter taking the form of radial and circular canals. The reproductive products are discharged externally, and are very commonly, though not always, of ectodermal origin.

Many Hydrozoa agree with Obelia in exhibiting alternation of generations, the asexual generation being represented by a fixed, more or less branched, hydroid

colony, the sexual generation by a free-swimming medusa. In other forms there are no free medusæ, but the hydroid colony produces fixed reproductive zooids. In others, again, there is no hydroid stage, the organism existing only in the medusa-form. Then, while in most instances the only skeleton or supporting structure is the horny perisarc, there are some forms in which the cœnosarc secretes a skeleton of calcium carbonate, forming a massive stony structure or coral. Lastly, there are colonial forms which, instead of remaining fixed, swim or float freely on the surface of the ocean, and such pelagic species are always found to exhibit a remarkable degree of polymorphism, *the zooids being of very various forms and performing diverse functions.*

Thus we have zoophyte colonies known to produce free medusæ, zoophyte colonies known not to produce free medusæ, and medusæ known to have no zoophyte stage. Moreover, there are many medusæ of which the life-history is unknown, so that it is uncertain whether or not a zoophyte stage is present. It is also found that in some cases closely allied zoophytes produce very diverse medusæ, while similar medusæ, in other cases, may spring from very different zoophytes. For these reasons a sort of double classification of the Hydrozoa has come about, some zoologists approaching the group from the point of view of the zoophyte, others from that of the medusa. On the whole the following scheme seems best adapted for bringing before the beginner the leading modifications of the class.

ORDER 1.—HYDROIDEA.

Hydrozoa in which there is a fixed zoophyte stage, and in which the sense-organs are exclusively ectodermal.

Sub-Order a.—Anthomedusæ (Athecata).

Hydroidea in which the polypes are not protected by hydrothecæ or the reproductive zooids by gonothecæ: the medusæ bear the gonads on the manubrium and have no lithocysts: frequently with marginal eye-spots.

Examples: *Bougainvillea* (Fig. 107), *Ceratella* (Fig. 109), *Hydra* (Fig. 110), *Protohydra* (Fig. 112).

Sub-Order b.—Leptomedusæ (Thecata).

Hydroidea in which hydro- and gonothecæ are present: the medusæ bear the gonads in connection with the radial canals and usually have either lithocysts or eye-spots.

Examples: *Obelia* (Fig. 99), *Clytia* (Fig. 115).

ORDER 2.—TRACHYLINÆ.

Hydrozoa in which no fixed zoophyte stage is known to occur, all members of the group being locomotive medusæ, some of which have been proved to develop directly from the egg. The marginal sense-organs are modified tentacles and consist partly of endoderm.

Sub-Order a.—Trachymedusæ.

Trachylinæ in which the tentacles spring from the margin of the umbrella, and the gonads are developed in connection with the radial canals.
Examples: Fig. 116.

Sub-Order b.—Narcomedusæ.

Trachylinæ in which the tentacles spring from the ex-umbrella, some distance from the margin, and the gonads are developed in connection with the manubrium.
Examples: Fig. 117.

ORDER 3.—HYDROCORALLINA.

Hydrozoa in which a massive skeleton of calcium carbonate is secreted from the cœnosarc, the dried colony being a coral. They are now often included among the athecate Hydroidea.

Example: *Millepora* (Fig. 120), *Stylaster* (Fig. 122).

ORDER 4.—SIPHONOPHORA.

Pelagic Hydrozoa in which the colony usually exhibits extreme polymorphism of its zooids.

Examples: *Halistemma* (Fig. 123), *Physalia* (Fig. 126).

ORDER 5.—GRAPTOLITHIDA.

An extinct group of Hydrozoa, found only in rocks of Palæozoic age, in the form of the fossilized perisarc of the branched colonies.

ORDER 6.—STROMATOPOROIDEA.

Fossil organisms probably belonging to the Hydrozoa; reef-builders in mid-palæozoic times.

ORDER 1.—HYDROIDEA.

The more typical members of this group agree in all essential respects with Obelia, consisting of branched colonies bearing two principal forms of zooids, which serve for nutritive and reproductive purposes respectively.

General Structure.—The form and size of the colonies are subject to great variation: they may be little insignificant tufts growing on shells, seaweeds, etc., or may take the form of complex trees three feet in height, and containing many thousand zooids. The hydranths may be colourless and quite invisible to the naked eye, or, as in some *Tubulariæ* (Fig. 108, 5), may be brilliantly coloured, flower-like structures, nearly an inch in diameter. The medusæ may be only just visible to the naked eye, or, as in *Æquorea*, may attain a diameter of 380 mm., or about 15 inches: they are often seen with great difficulty owing to the bubble-like transparency of the umbrella; but frequently the manubrium is brightly coloured, or brilliant dots of colour—the *ocelli* or eye-spots—may occur around the margin of the umbrella. They are also frequently

phosphorescent, the phosphorescence of the ocean being often due to whole fleets of medusæ liberated in thousands from the hydroid colonies beneath the surface.

The two sub-orders of Hydroidea are distinguished by the arrangement of the **perisarc**. In the Anthomedusæ, of which *Bougainvillea* (Fig. 107) is a good example, the cuticle stops short at the bases of the hydranths, and the repro-

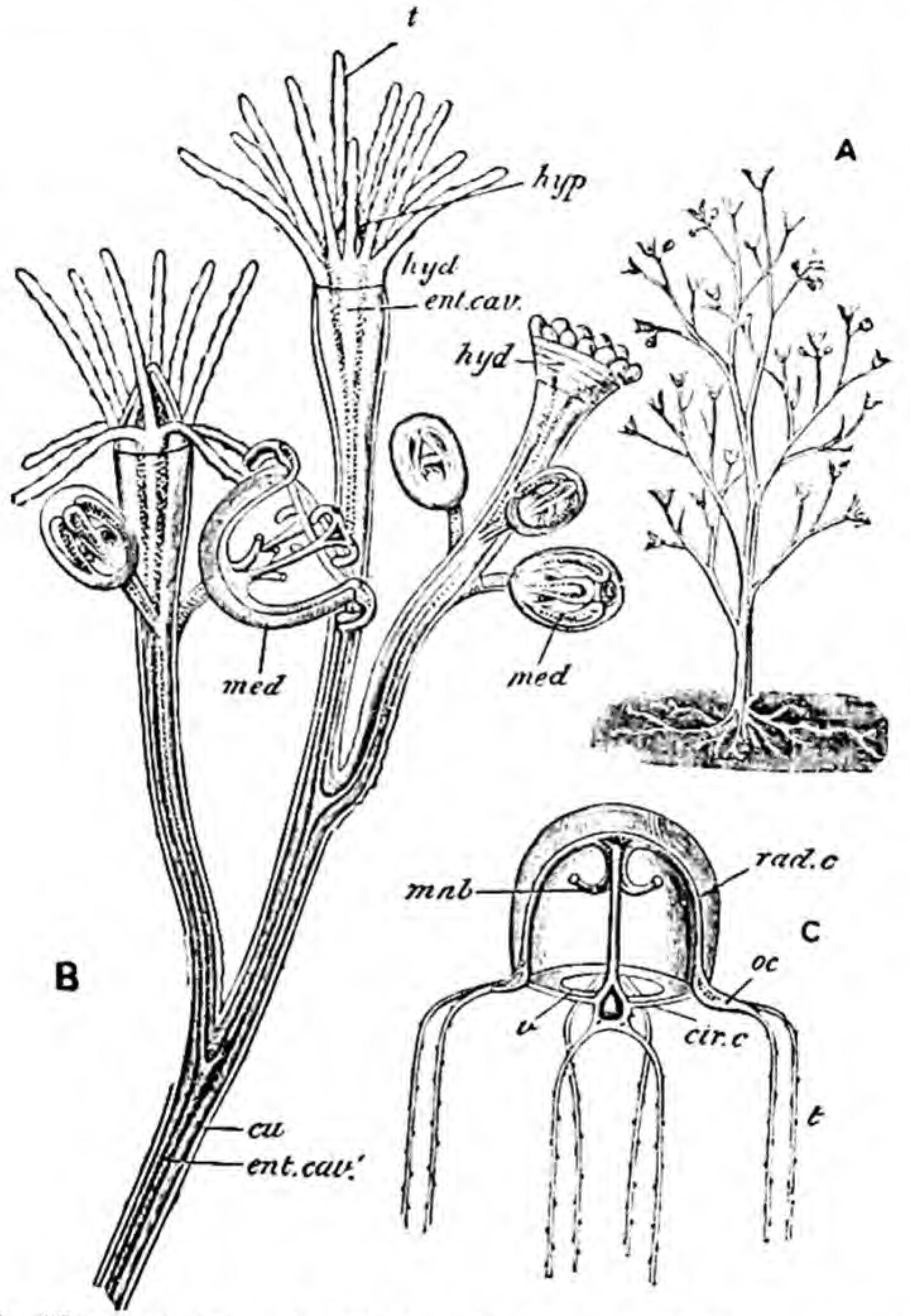


FIG. 107.—**Bougainvillea ramosa.** *A*, entire colony, natural size; *B*, portion of the same magnified; *C*, immature medusa. *cir. c.* circular canal; *cu.* cuticle or perisarc; *ent. cav.* enteric cavity; *hyd.* polype or hydranth; *hyp.* hypostome or manubrium; *med.* medusa; *mnb.* manubrium; *rad. c.* radial canal; *t.* tentacle; *v.* velum. (From Parker's *Biology*, after Allman.)

ductive zooids are not enclosed in gonothecæ. It is for this reason that, in classifications founded on the zoophyte stage, the Anthomedusæ are called *Athecata* (*Gymnoblastea*) (see also Fig. 108, *1*, *4*, *5*). In the Leptomedusæ the cuticle is usually of a firmer consistency than in the first sub-order, and furnishes hydrothecæ for the hydranths and gonothecæ for the reproductive zooids: they are hence often classified as *Thecata* (*Calyptoblastea*). To this group

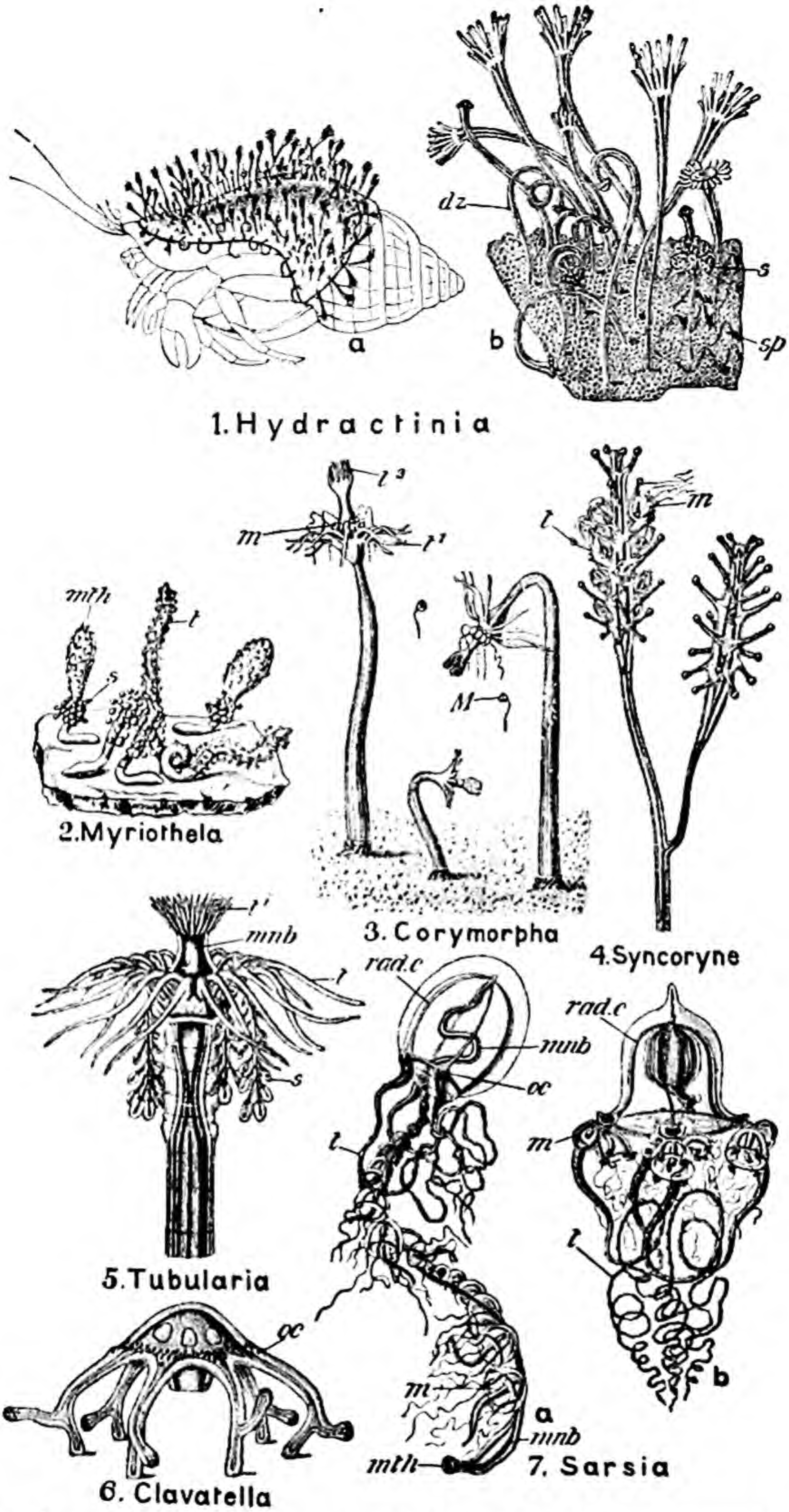


FIG. 108.—Various forms of **Anthomedusae (Athecata).** In *1*, *a* shows the entire colony, *b* a portion highly magnified; in *7*, *a* is a species producing medusa-buds from the manubrium, *b* from the bases of the tentacles; *dz.* dactylozooids; *m.* and *M.* medusæ; ***mnb.*** manubrium; ***mth.*** mouth; *oc.* eye-spots; ***rad. c.*** radial canals; *s.* sporosacs; ***sp.*** spines; ***t.***, ***t*¹.**, ***t*³**, tentacles.

belong the commonest species of hydroids found on the seashore, and often mistaken for seaweeds—the "Sea-firs" or Sertularians.

The **medusæ** also exhibit characteristic differences in the two sub-orders. In the Anthomedusæ the umbrella is usually strongly arched, and may even be conical or mitre-shaped (Figs. 107, 108, *7*; 112, *1* and *2*): its walls are thick, owing to a great development of the gelatinous mesoglœa of the ex-umbrella, that of the sub-umbrella remaining thin; and the velum is considerably wider than in Obelia. But the most important characteristics are the facts that the gonads (*gon.*) are developed on the manubrium and that lithocysts are absent. Sense-organs are, however, present in the form of specks of red or black pigment at the bases of the tentacles. These *ocelli* (*oc.*) consist of groups of ectoderm cells containing pigment and it has been proved experimentally that they are sensitive to light: they are, in fact, the simplest form of eyes. In the Leptomedusæ the umbrella is usually less convex, thinner, and of softer consistency than in the Anthomedusæ, the gonads are developed as buds formed in connection with the radial canals and projecting from the sub-umbrella, the velum is feebly developed, and sense-organs take the form sometimes of ocelli, but usually of lithocysts.

In the majority of Hydroidea the **cœnosarc**, as in Obelia, consists of a more or less branched structure attached to stones, timber, seaweed, shells, etc., by a definite root-like portion (*hydrorhiza*). The curious genus *Hydractinia* (Fig. 108, *1*) is remarkable for possessing a massive cœnosarc, consisting of a complex arrangement of branches which have undergone fusion, so as to form a firm brownish crust on the surfaces of dead gastropod shells inhabited by Hermit-crabs. The constant association of Hydractinia with Hermit-crabs is a case of *commensalism*: the hydroid feeds upon minute fragments of the Hermit-crab's food, and is thus its commensal; and the Hermit-crab is protected from its enemies by the presence of the inedible, stinging hydroid. Hydractinia belongs to the Anthomedusæ: *Clathrozoon*, an Australian genus, resembles it in having branched and intertwined cœnosarcal tubes, the perisarc of which undergoes fusion; but the complex mass thus produced, instead of forming an incrustation on a shell, is a large, abundantly branched, tree-like structure, resembling some of the fan-corals or Gorgonaria (*vide* p. 190). *Ceratella* (Fig. 109) has a similar fan-coral-like appearance, with a branching axis composed of numerous intertwining and anastomosing tubes.

A great simplification of the colony is produced in *Myriothela* (Fig. 108, *2*), in which the short cœnosarc bears a single large terminal hydranth, and gives off numerous slender branches which bear the reproductive zooids (*s.*). Even greater simplicity is found in *Corymorpha* (*3*), in which the entire organism consists of a single-stalked polype, from the tentacular region of which the medusæ (*m.*) arise.

But the simplest members of the whole class, with the exception of one or two imperfectly known forms which will be referred to below, are the Fresh-water Polypes of the genus *Hydra*. The entire organism (Figs. 32 and 110) consists of a simple cylindrical body with a conical hypostome and a circlet of six or eight tentacles. It is ordinarily attached, by virtue of a sticky secretion from the proximal end, to weeds, etc., but is capable of detaching itself and moving from place to place after the manner of a looping caterpillar. There is no perisarc. The tentacles are hollow, and communicate freely with the cœlenteron.

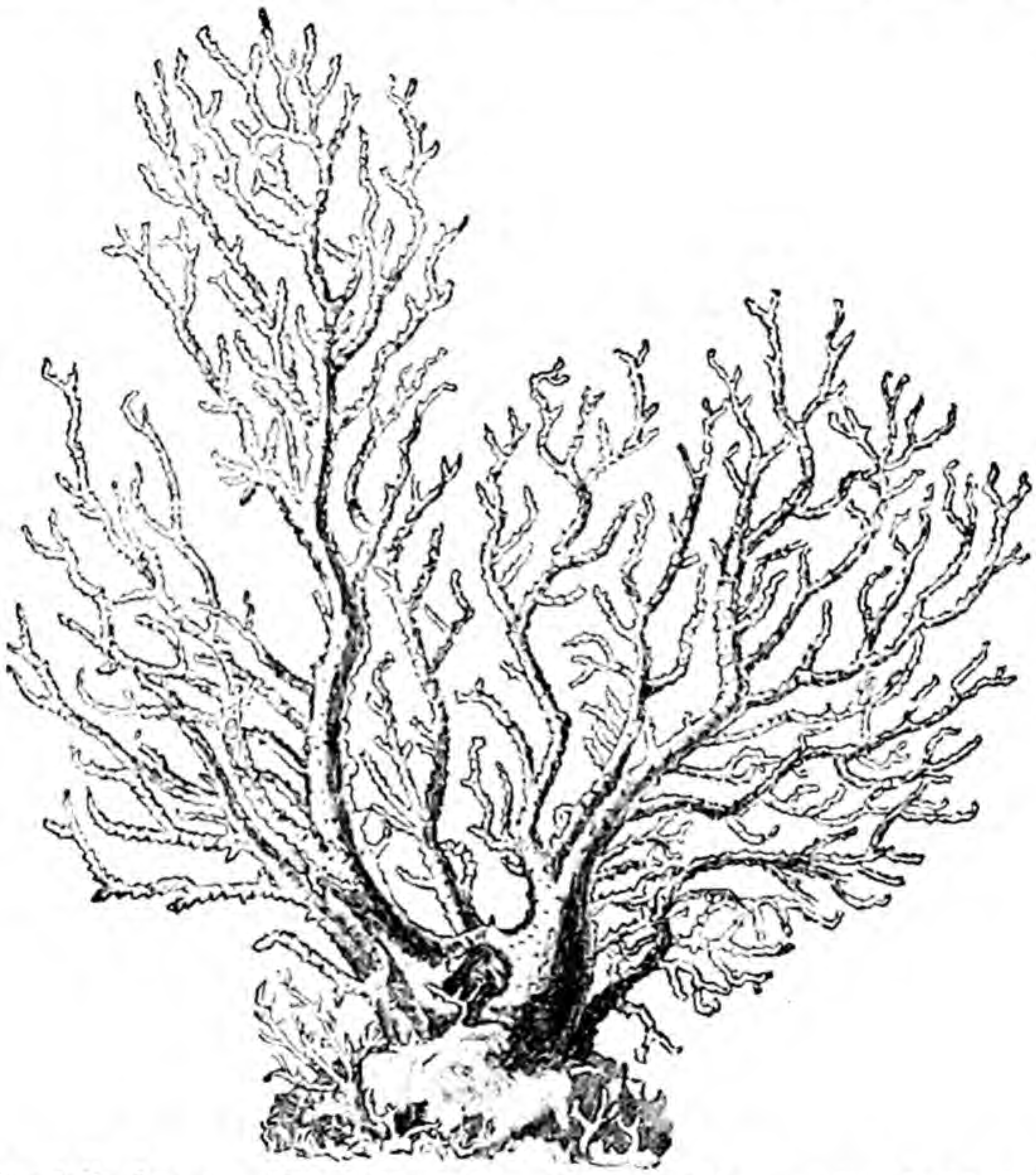


FIG. 109.—**Ceratella fusca.** About nat. size. (From Hickson, after Baldwin Spencer.)

Both the body and the tentacles are highly contractile, the contractions being effected by means of a layer of fibres which run longitudinally. These fibres are processes—the *muscle processes*—(*C, m. pr.*) of the large ectoderm cells. Similar shorter muscle processes of some of the endoderm cells run circularly and antagonize the longitudinal fibres. Cells thus combining the muscular with the epithelial character are called musculo-epithelial cells. Nematocysts are abundant in the ectoderm. The endoderm cells are mostly amœboid and vacuolated. Each usually bears one or more flagella, but these may be retracted. Glandular cells occur here and there.

Nerve-cells (multipolar) and sensory cells occur in both layers. The nerve-cells communicate with each other to form the most primitive type of nervous system, a so-called *nerve-net* (Fig. 111). Wherever at the surface of the animal

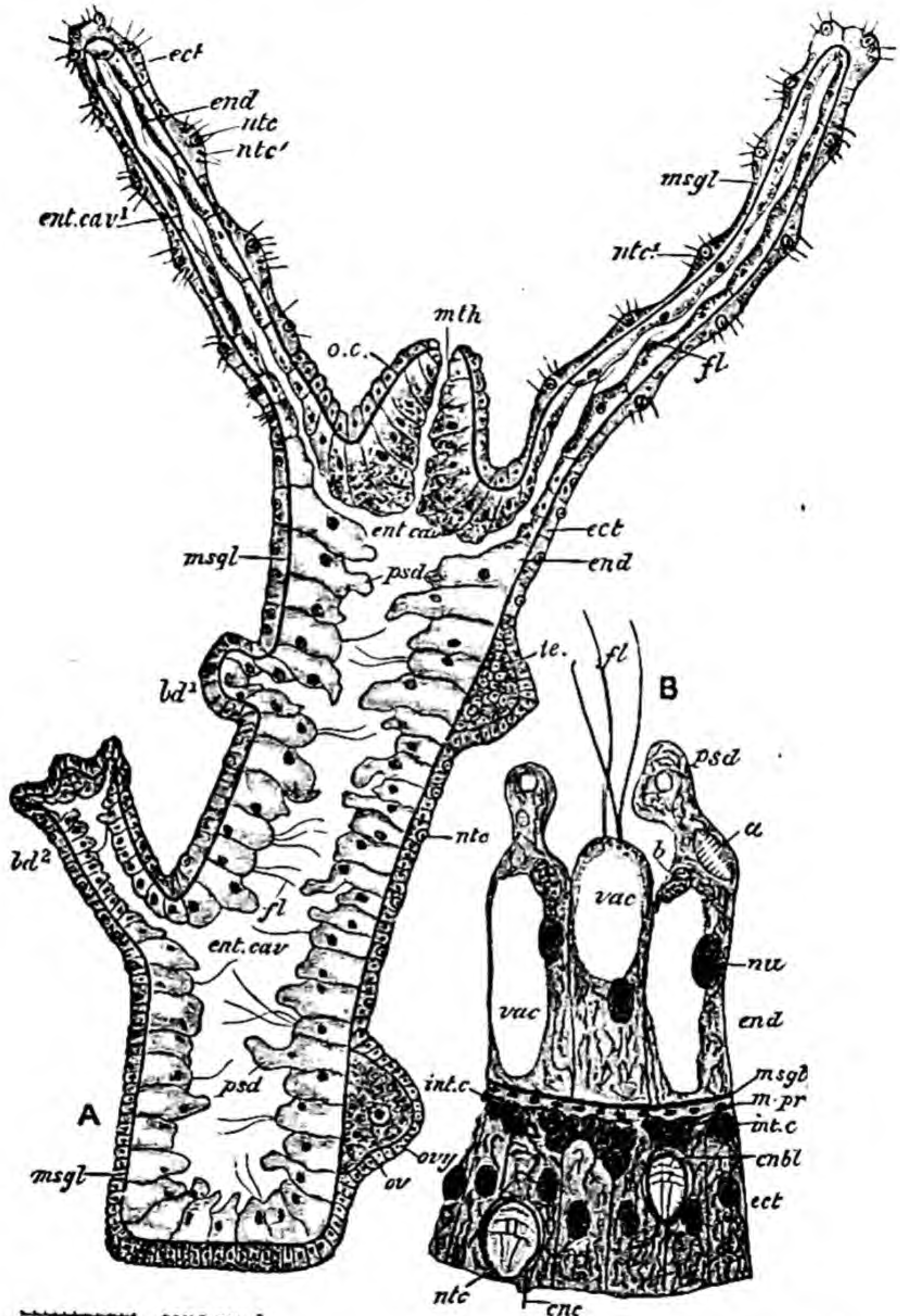


FIG. 110.—**Hydra.** *A*, vertical section of entire animal; *B*, portion of transverse section, highly magnified; *a*, ingested diatom; *bd. 1*, *bd. 2*, buds; *ent. cav.* enteric cavity; *ent. cav'*. its prolongation into the tentacles; *fl.* flagellum; *int. c.* interstitial cells; *m. pr.* muscle-processes; *mth.* mouth; *msgl.* mesoglœa; *ntc.* large, *ntc'.* small nematocysts; *nu.* nucleus; *o. c.* oral cone; *ov.* ovum; *ovy.* ovary; *psd.* pseudopods; *te.* testis; *vac.* vacuole. (From Parker's *Elementary Biology*, after Lankester and Howes.)

sensory cells are stimulated mechanically, chemically, or by changes in the illumination, the stimulus is handed on to the nerve-net, in which its effect is *diffusely* propagated to the contractile elements of both ectoderm and endoderm,

causing them to contract. The simplest response of the animal to external stimulation is thus a protective contraction of the whole body.

Buds (Fig. 110, *bd. 1*, *bd. 2*) are produced which develop into Hydræ, but these are always detached sooner or later, so that a permanent colony is never formed. There are no special reproductive zooids, but simple ovaries (*ovy.*) and testes (*te.*) are developed, the former at the proximal, the latter at the distal end of the body. Even simpler than Hydra is *Protohydra* (Fig. 112), in which the tentacles are absent.

FIG. 111.—Nerve-net of **Hydra.** (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer).)

Pelagohydra is also solitary, but is pelagic. The part corresponding to the base in Hydra here takes the form of a float, and there are tentacles distributed over the surface of the float as well as in the neighbourhood of the mouth ; medusæ are developed from processes on the float. Pelagohydra, however, is perhaps more nearly related to the *Siphonophora* —an order yet to be dealt with—than to the Hydroidea.

The **polypes** are usually cylindrical, as in Obelia, but in some genera they are widened out into a vase-like form (Fig. 108, *5*), in others elongated into a spindle-shape (*4*). The tentacles may be disposed in a single circlet, as in Obelia and Hydra, or there may be an additional circlet round the hypostome (*3*, *5*), or at the base of the polype, or they may be scattered irregularly over the whole surface (*4*). In Myriothela (*2*) they are short, and so numerous as to have the appearance of close-set papillæ. In some forms they are knobbed at the ends, the knobs being loaded with stinging-capsules (*4*).

In some species a *dimorphism* of the hydranths obtains, some of them being modified to form protective zooids. In Hydractinia (*1*) these are simply mouthless hydranths with very short tentacles abundantly supplied with nematocysts, capable of very active movements, and called *dactylozooids* (*dz.*). In Plumularia there are small structures called "guard-polypes," resembling tentacles in structure, with very numerous nematocysts, and each enclosed in

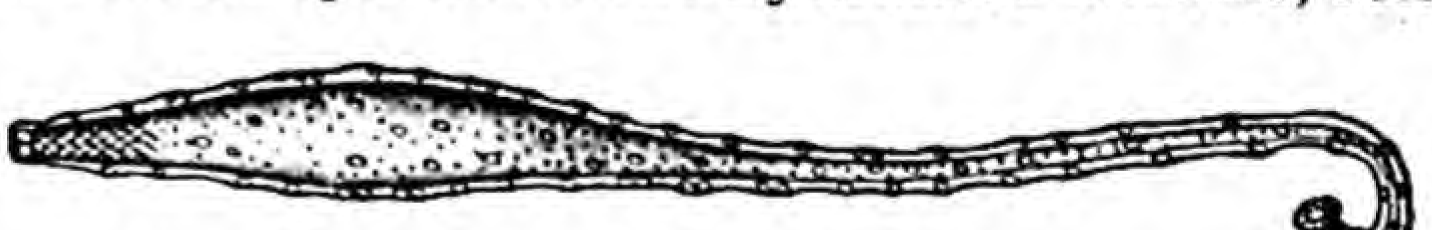


FIG. 112.—**Protohydra leuckartii.** (From Chun, after Greeff.) The mouth is to the left, the disc of attachment to the right.

a theca. In Hydractinia the cœnosarc is also produced into spines (*sp.*), which may be much modified zooids.

But the most remarkable modifications occur in the **reproductive zooids**. In a large proportion of genera, both of Anthomedusæ and Leptomedusæ, these take the form of locomotive medusæ, agreeing in general structure with the descriptions already given. Each appears at first as a hollow bud-like process of the blastostyle, or of an ordinary polype, or, more exceptionally, of the cœnosarc. This becomes constricted at the junction and rounded off. The ectoderm at its free extremity becomes thickened, and this thickening, as it grows, pushes the endoderm before it, producing a sort of involution. In the interior of the mass of ectoderm a cavity appears: this is destined to form the sub-umbrellar cavity. The ectodermal partition that at first separates the cavity from the exterior becomes perforated and most of it is absorbed, what remains round the edge going to form the velum. The endoderm is reduced to a thin layer except along four radial lines where it gives rise to the four radial canals, the thin parts between going to form the endoderm lamella.

In different families and genera the medusæ exhibit almost endless variety in detail. As to size they vary from about 1 mm. in diameter up to 400 mm. (16 inches). The number of marginal tentacles may be very great (Fig. 113, *2*), or these organs may be reduced to two (Fig. 113, *1*), or even to one (Fig. 108, *3*); in the last-named cases it will be noticed that the medusa is no longer radially but bilaterally symmetrical, *i.e.*, it can be divided into two equal and similar halves by a single plane only—viz., the plane passing through the one or two tentacles. With the increase in the number of the tentacles a corresponding increase in that of the radial canals often takes place (Fig. 113, *3*). In addition to the marginal tentacles longer or shorter *oral tentacles* may be present in a whorl surrounding the mouth (Fig. 113, *t'*.).

Some medusæ creep over submarine surfaces, walking on the tips of their peculiarly modified tentacles (Fig. 108, *6*), but the majority propel themselves through the water in a series of jerks by alternately contracting and expanding the umbrella, and so, by rhythmically driving out the contained water, moving with the apex foremost. In correspondence with these energetic movements there is a great development of both muscular and nervous systems. The velum and the sub-umbrella possess abundance of muscle-fibres, presenting a transverse striation, and round the margin of the umbrella is a double ring of nerve-cells and fibres, one ring being above, the other below the atttachment of the velum (Fig. 104, *D, nv., nv.'*). The medusæ thus furnish the first instance we have met with of a *central nervous system, i.e.*, a concentration of nervous tissue over a limited area serving to control the movements of the whole organism. It has been proved experimentally that the medusa is paralysed by removal of the nerve-ring. Over the whole sub-umbrella is a loose network of nerve-cells and fibres connected with the nerve-ring, and forming a nerve-net.

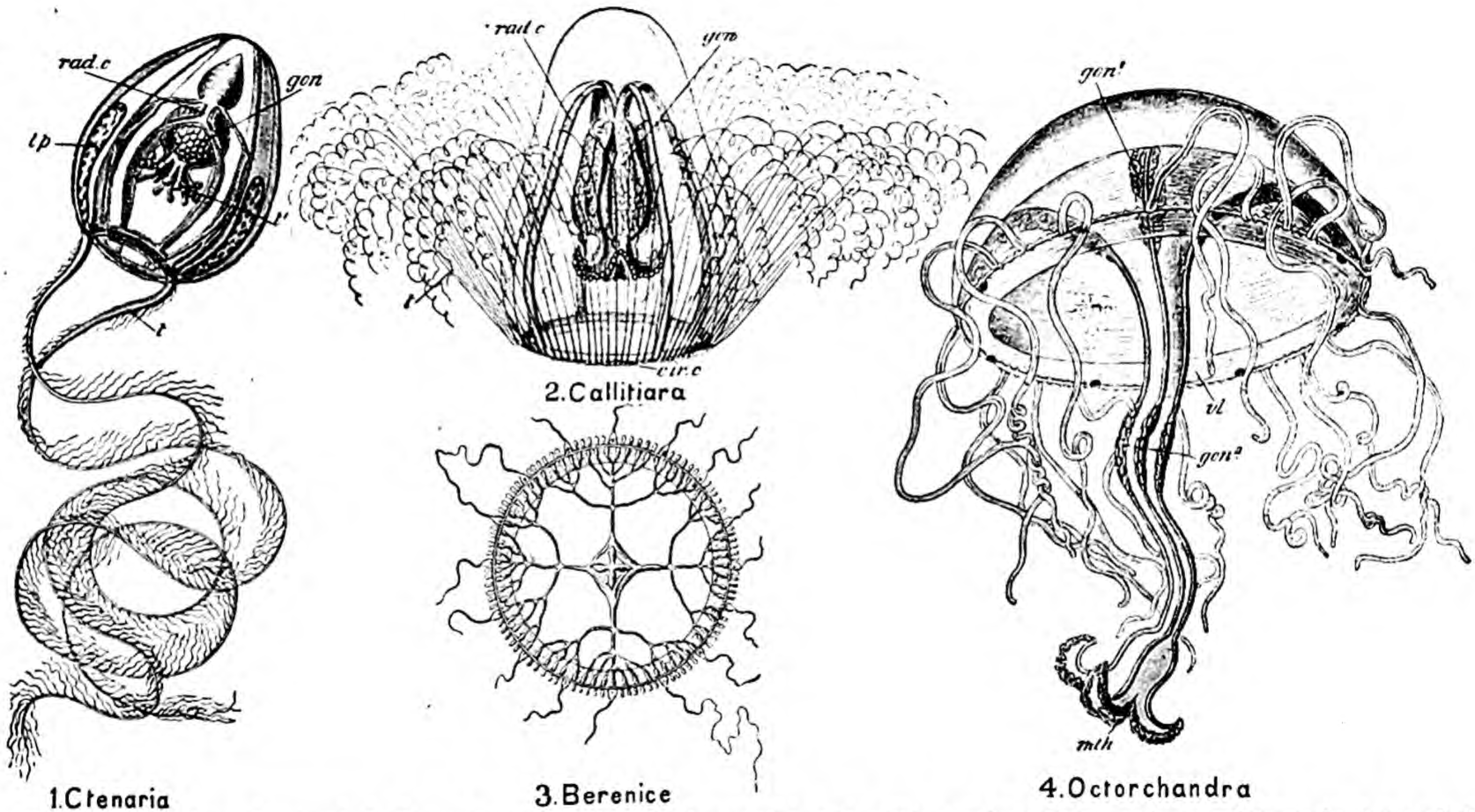


FIG. 113.—Various forms of **Anthomodusæ.** *cir. c.* circular canal; *gon.*, *gon*¹., *gon*²., gonads; *rad. c.* radial canal; *t.* marginal tentacles; *t'.* oral tentacles; *t. p.* tentacle pouch; *vl.* velum. (After Haeckel.)

In some medusæ the circular canal communicates with the exterior by minute pores placed at the summits of papillæ, the endoderm cells of which contain brown granules. There seems to be little doubt that these are *organs of excretion*, the cells withdrawing nitrogenous waste-matters from the tissues and passing them out through the pores. If we except the contractile vacuoles of Protozoa, this is the first appearance of specialized excretory organs in the ascending series of animals.

Besides producing gonads, some medusæ multiply asexually by budding, the buds being developed either from the manubrium (Fig. 108, *7a*), or from the margin of the umbrella (*7b*) or the base of the tentacles: in one case they are formed on blastostyles developed on the gonads. The buds always have the medusa form.

In many Hydroidea the reproductive zooids undergo a degradation of structure, various stages of the process being found in different species. Almost

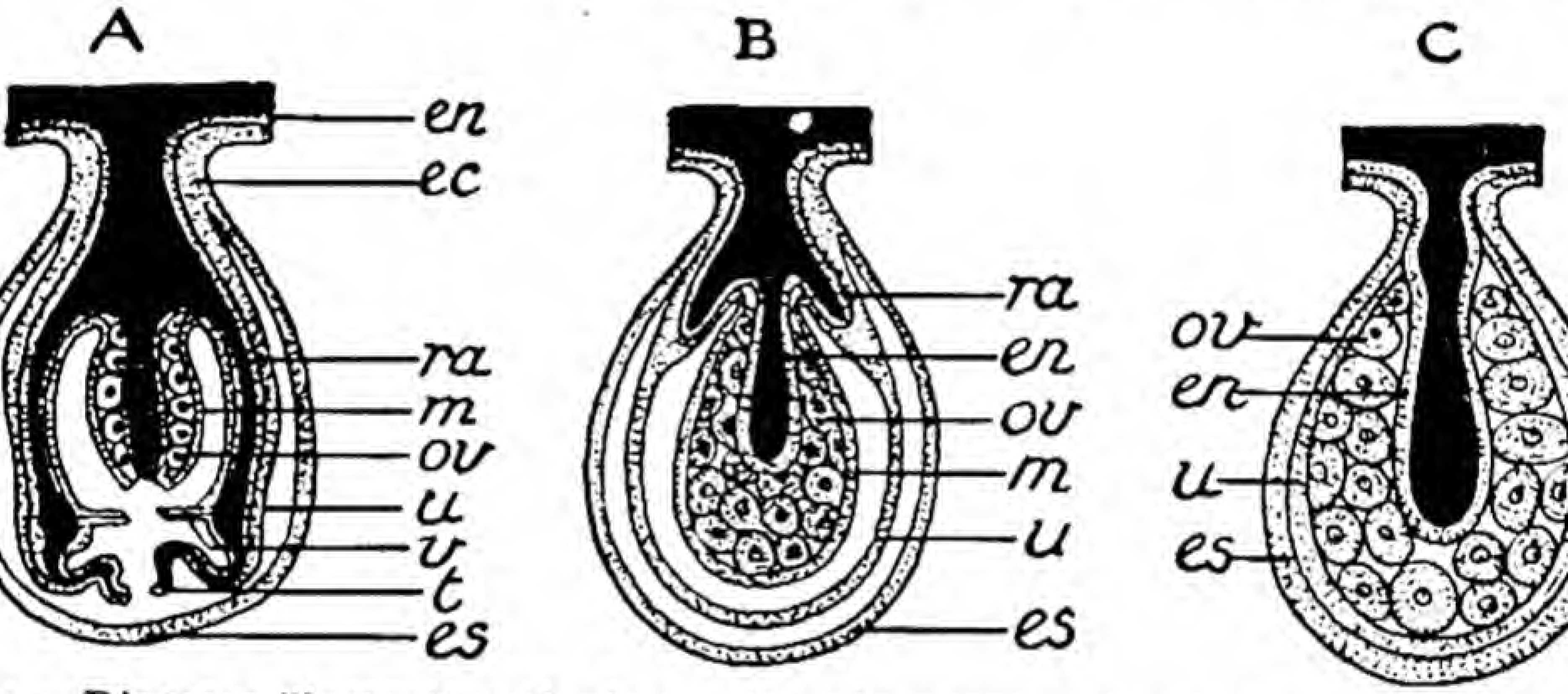


FIG. 114.—Diagram illustrating the formation of a sporosac by the degradation of a medusa. *A*, medusa enclosed in ectodermal envelope (*es*); *B*, intermediate condition with vestiges of umbrella (*u*) and radial canals (*ra*); *C*, sporosac. *ec.* ectoderm; *en.* endoderm; *m.* manubrium; *ov.* ovary; *t.* tentacle; *v.* velum. (From Lang's *Comparative Anatomy*.)

every gradation is found, from perfect medusæ to ovoid pouch-like bodies called *sporosacs* (Fig. 108, *1b*, *5*, *s.*), each consisting of little more than a gonad, but showing an indication of its true nature in a prolongation of the digestive cavity of the colony, representing the stomach of the manubrium (Fig. 114). We thus have a reproductive *zooid* reduced to what is practically a reproductive *organ*. It is obvious that a continuation of the same process might result in the production of a simple gonad like that of Hydra: there is, however, no evidence to show that the Fresh-water Polype ever produced medusæ, and the probabilities are that its ovaries and testes are simply gonads, and not degenerate zooids. The case is interesting as showing how a simple structure may be imitated by the degradation of a complex one. It is quite possible, on the other hand, that the reproductive organs of the Leptomedusæ (Fig. 104) are sporosacs, *i.e.*, reproductive zooids, not mere gonads. In some rare cases the sexual cells are not developed either in medusæ or in sporosacs, but are formed directly in the blastostyles.

In Obelia we found the medusæ to be budded off from peculiarly modified mouthless zooids—the blastostyles. This arrangement, however, is by no means universal: the reproductive zooids—whether medusæ or sporosacs—may spring directly from the cœnosarc, as in Bougainvillea (Fig. 107), or from the ordinary hydranths (Fig. 108, *4* and *5*). The primitive sex-cells, from which ova or sperms are ultimately developed, are sometimes formed from the endoderm or (more usually) ectoderm cells of the reproductive zooid; but in many cases they originate in the cœnosarc, and slowly migrate to their destination in the ectoderm of the gonad, where they metamorphose in the usual way into the definitive reproductive products, which when mature pass into the space below the ectoderm of the gonad.

The **development** of the Hydroidea frequently, but not always, begins within the maternal tissues, *i.e.*, while the fertilized egg is still contained in the gonad of the medusæ or in the sporosac. The zygote divides into two cells, then into

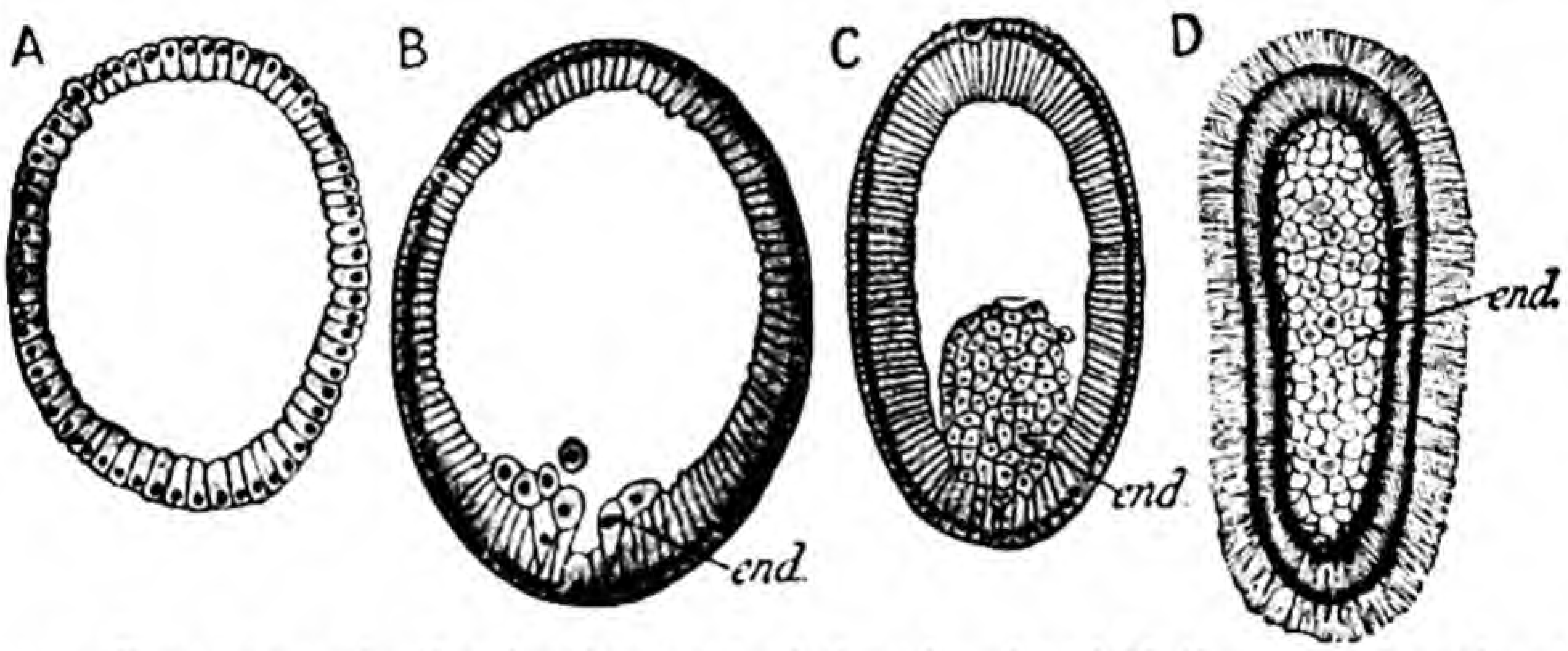


FIG. 115.—Four stages in the development of the planula of **Clytia.** *A*, blastula stage; *B*, formation of endoderm by immigration of cells of blastula wall at one pole; *C*, endoderm, a solid mass, half filling the cavity of the blastula; *D*, free-swimming planula larva; *end.* endoderm. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Metschnikoff.)

four, eight, sixteen, etc. Fluid accumulates in the interior of the embryo, resulting in the formation of a blastula or hollow globe formed of a single layer of cells (Fig. 115, *A*). The blastula elongates, and the cells at one pole undergo division, the daughter-cells passing into the cavity, which they gradually fill (*B*, *C*). At this stage the embryo is called a *planula* (*D*): it consists of an outer layer of cylindrical cells—the ectoderm—which acquire cilia, and an inner mass of polyhedral cells—the endoderm. In some cases the planula arises by a different process: a solid morula is formed, the superficial cells of which become radially elongated and form ectoderm, the central mass of cells giving rise to endoderm. By means of its cilia, the planula swims freely for a time, after which it comes to rest, fixing itself at one end to some suitable support. Before long a cavity appears in the middle of the solid mass of endoderm, the cells of which then arrange themselves in a single layer around the cavity or cœlenteron. The animal becomes converted into a simple polype or ***hydrula***

by the attached end broadening into a disc and the opposite extremity forming a manubrium and tentacles. The hydrula soon begins to send off lateral buds, and so produces the branched colony.

In Tubularia the zygote develops, while still enclosed in the sporosac, into a short hydrula, which, after leading a free existence for a short time, fixes itself by its proximal end, buds, and produces the colony. In Hydra development begins in the ovary, and is complicated by the fact that the ectoderm of the morula gives rise to a sort of protective shell: in this condition the embryo is set free, and, after a period of rest, develops into the adult form.

ORDER 2.—TRACHYLINÆ.

General Structure.—The members of this order are all medusæ: with a few exceptions they develop directly from the egg into the medusa without passing through a polype stage. They thus differ from the members of the preceding order in the fact that no alternation of generations ordinarily occurs in their life-history.

Most species are of small or moderate size, the largest not exceeding 100 mm. (4 inches) in diameter. The gelatinous tissue or mesoglœa of the ex-umbrella is usually well developed, giving the medusa a more solid appearance than the delicate jelly-fish of the preceding order: this is well shown in Fig. 116 in which the apical region of the umbrella has a comparatively immense thickness. The tentacles are also stiff and strong, and are always solid in the young condition, although they may be replaced in the adult by hollow tentacles.

But the most characteristic anatomical feature of the group is the structure of the **sense-organs,** which are club-shaped bodies (Figs. 116 and 117, *tc.*) consisting of an outer layer of ectoderm enclosing a central axis of endoderm cells (Fig. 118): they have, therefore, the structure of tentacles. They contain one or more calcareous bodies, which are always derived from the endoderm. To distinguish them from the lithocysts of Leptomedusæ, and to mark the fact that they are modified tentacles, they are called *tentaculocysts*. They may either project freely from the margin of the umbrella, or may become enclosed in a pouch-like growth of ectoderm and more or less sunk in the tissue of the umbrella. Eyes occur in some, and are always of simple structure.

The two sub-orders of Trachylinæ are characterized by the mode of origin of the **tentacles.** In Trachymedusæ, as in the preceding order, they arise near the edge of the umbrella (Fig. 116), but in the Narcomedusæ they spring about halfway between the edge and the vertex (Fig. 117), and are continued, at their proximal ends, into the jelly of the ex-umbrella in the form of "tentacle-roots" (*t.r.*).

As to the position of the **reproductive organs,** there is the same difference between the two sub-orders of Trachylinæ as between the two sub-orders of Hydroidea. In the Trachymedusæ the gonads (Fig. 116, *gon.*) are developed in

the course of the radial canals; in the Narcomedusæ (Fig. 117) they lie on the manubrium, sometimes extending into the pouch-like offshoots of its cavity.

There is always a well-developed velum, which, as in Fig. 117, *1*, may hang

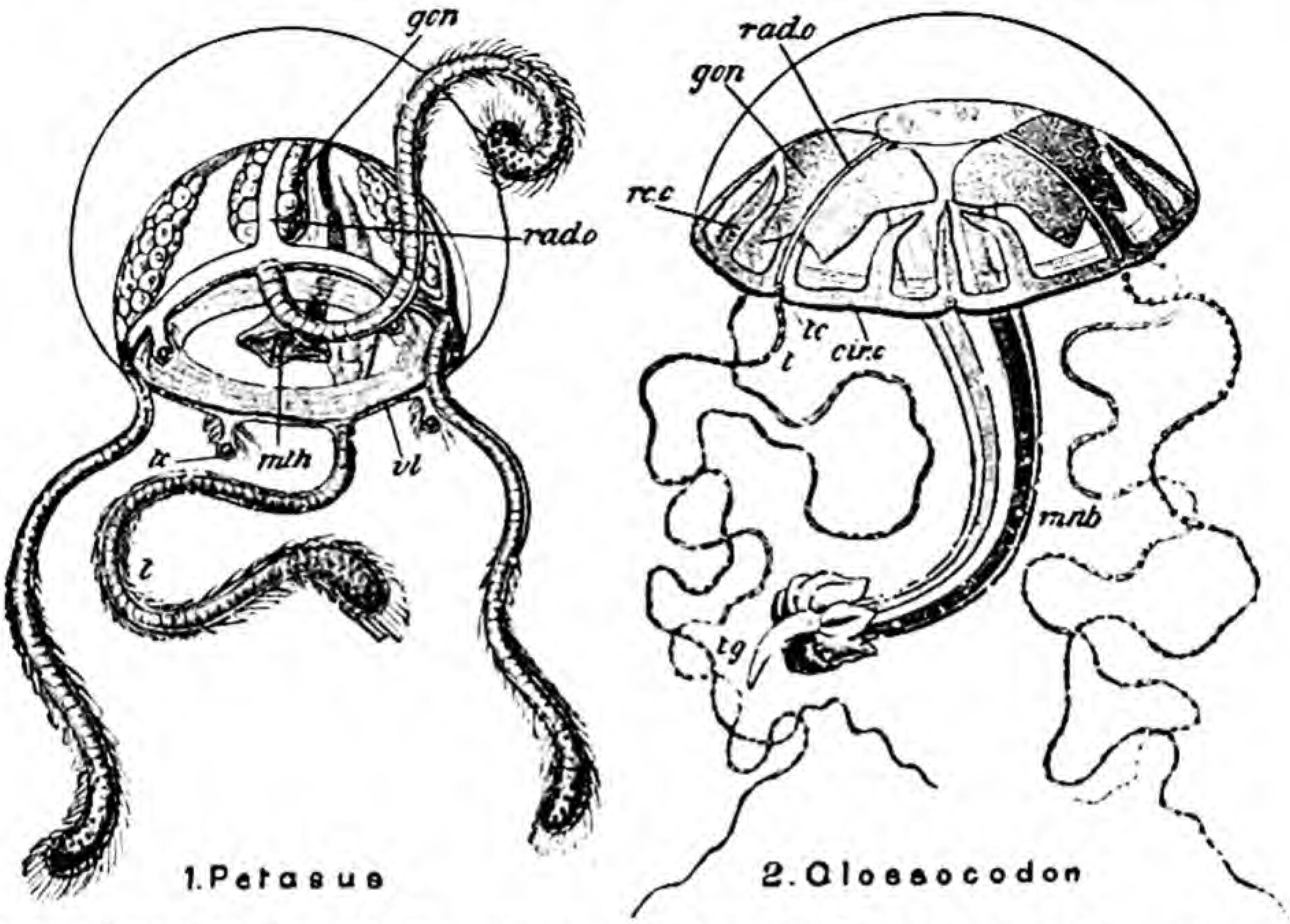


FIG. 116.—Two **Trachymedusæ.** *cir. c.* circular canal; *gon.* gonad; *mnb.* manubrium; *mth.* mouth; *rad. c.* radial canal; *rc. c.* recurrent canal; *t.* tentacle; *tc.* tentaculocyst; *tg.* tongue; *vl.* velum. (After Haeckel.)

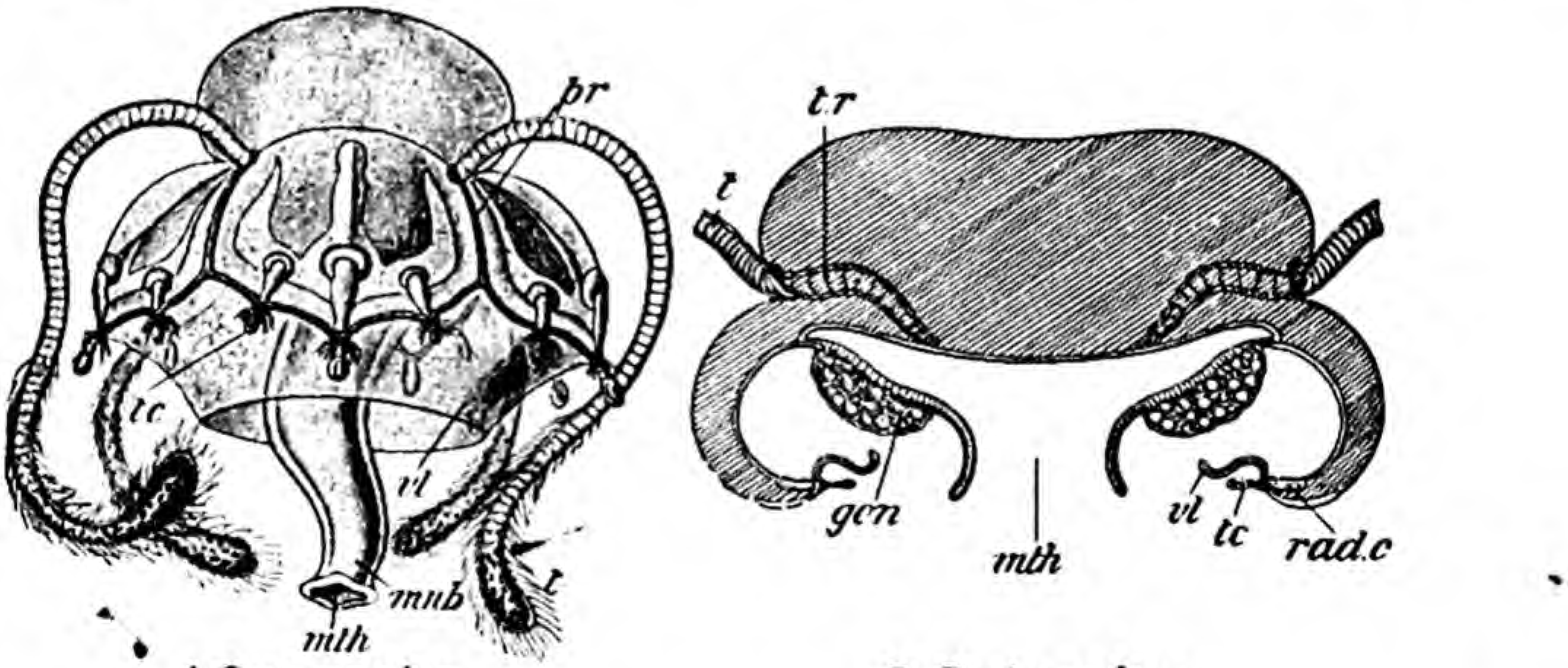


FIG. 117.—Two **Narcomedusæ,** *2* in vertical section. *gon.* gonad; *mnb.* manubrium; *mth* mouth; *pr.* peronium; *rad. c.* radial canal; *t.* tentacle; *tc.* tentaculocyst; *t.r.* tentacle-root; *vl.* velum. (After Haeckel.)

down vertically instead of taking the usual horizontal position. In the Narcomedusæ the manubrium is short; in the Trachymedusæ it is always well developed, and is sometimes (Fig. 116, *2*) prolonged into a long, highly contractile peduncle, having its inner surface produced into a tongue-like process

(*tg.*) which protrudes through the mouth. In some the gastric cavity is situated in the manubrium, which in such a case is looked upon as partly of the nature of a process of the sub-umbrella (*pseudo-manubrium*).

The simplest case of the **development** of Trachylinæ is seen in *Æginopsis*, one of the Narcomedusæ. The zygote gives rise to a ciliated planula, which forms first two (Fig. 119), then four tentacles, and a mouth, hypostome, and stomach. The larva of Æginopsis is thus a *hydrula*, closely resembling the corresponding stage of Tubularia. After a time the tentacular region grows out, carrying the tentacles with it, and becomes the umbrella of the medusa. Thus the actual formation of the medusa from the hydrula of Æginopsis corresponds precisely with the theoretical derivation given above (p. 131). It will be seen that in the present case there is no metagenesis or alternation of generations,

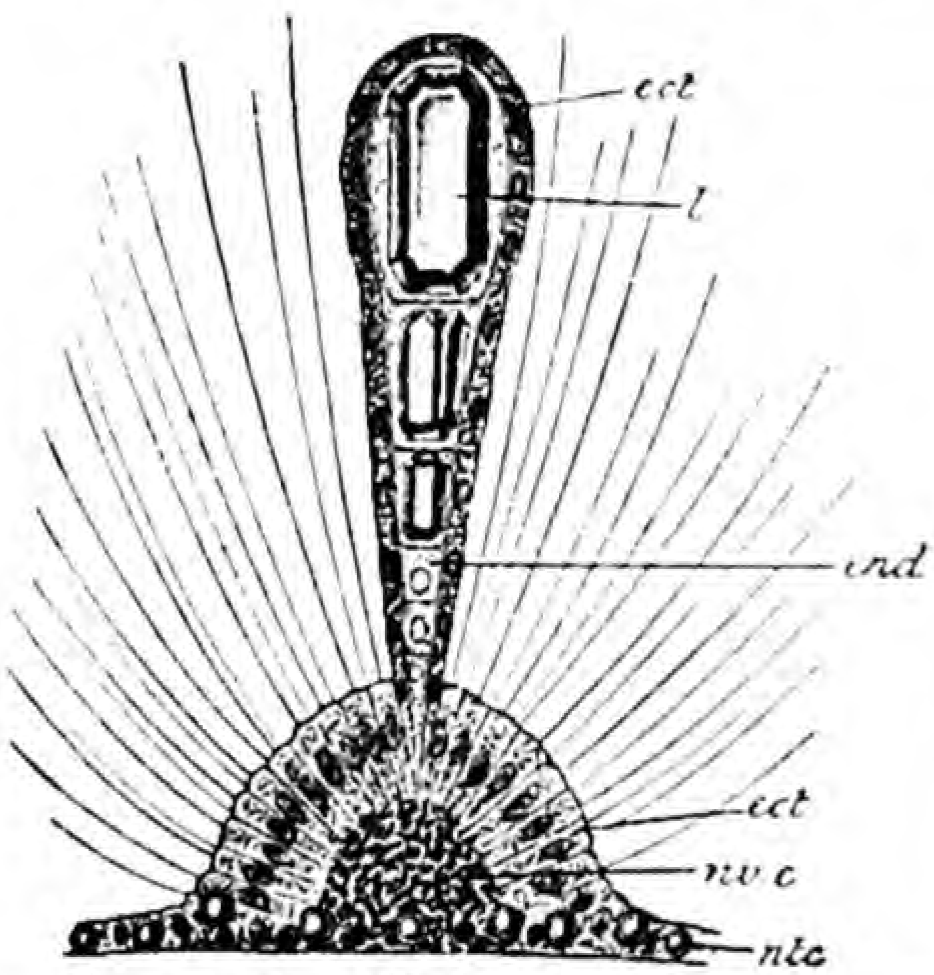


FIG. 118.—**Æginura myosura,** a tentaculocyst highly magnified. *ect.* ectoderm; *end.* endoderm; *l.* calcareous bodies; *ntc.* nematocysts; *nv. c.* group of nerve-cells. (After Haeckel.)

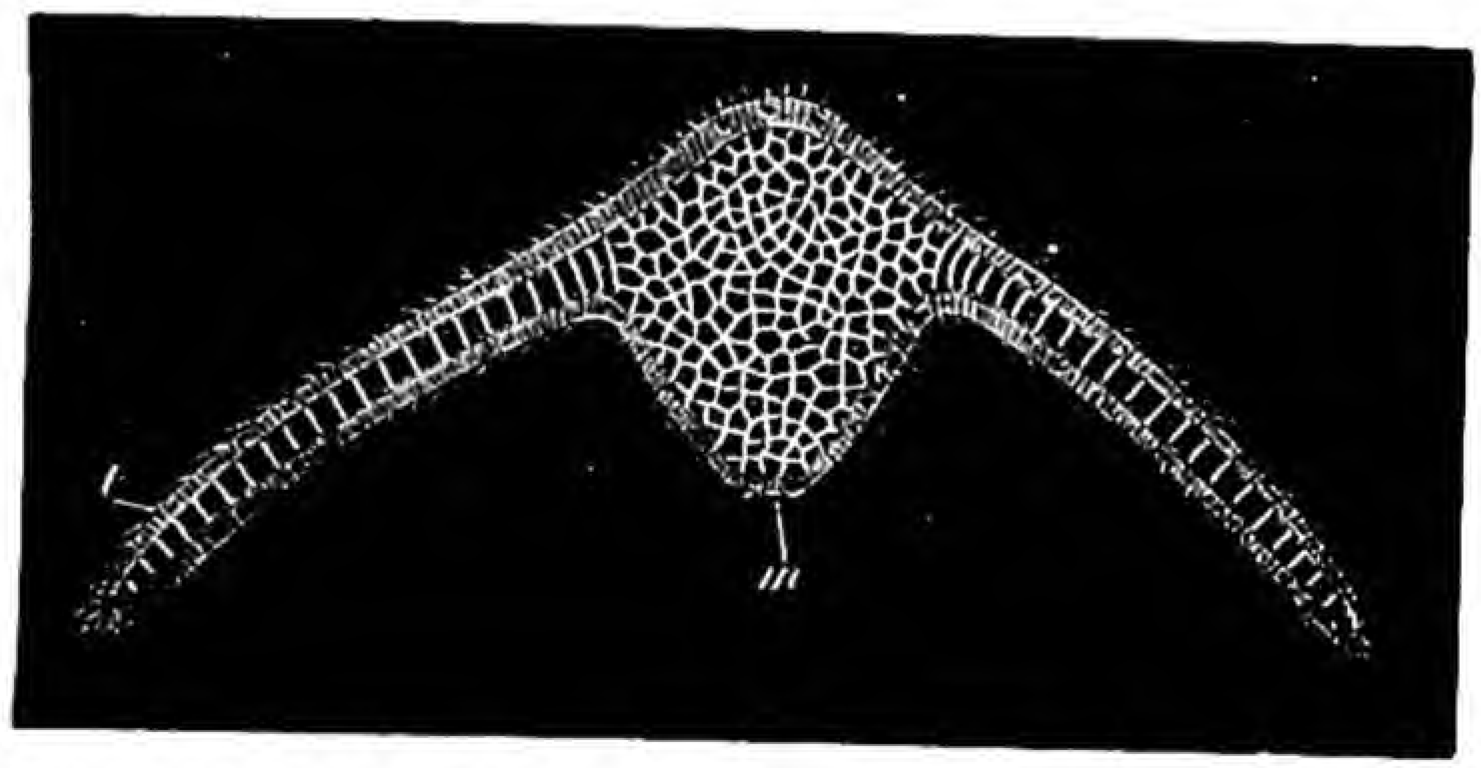


FIG. 119.—Larva of **Æginopsis.** *m.* mouth; *t.* tentacle. (From Balfour, after Metschnikoff.)

but that development is accompanied by a *metamorphosis*—that is, the egg gives rise to a larval form differing in a striking manner from the adult, into which it becomes converted by a gradual series of changes.

ORDER 3.—HYDROCORALLINA.

The best-known genus of Hydroid Corals is *Millepora*, one species of which is the beautiful Elk-horn Coral, *M. alcicornis*. The dried colony (Fig. 120, *A*) consists of an irregular lobed or branched mass of carbonate of lime (*corallum*), the whole surface beset with the numerous minute pores to which the genus owes its name. The pores are of two sizes: the larger are about 1 or 2 mm. apart, and are called *gastropores* (*B, g.p.*); the smaller are arranged more or less irregularly round the gastropores, and are called *dactylopores* (*d.p.*). The whole surface of the coral between the pores has a pitted appearance. Sections

(*C*) show that the entire stony mass is traversed by a complex system of branched canals, which communicate with the exterior through the pores. The wide vertical canals in immediate connection with the pores are traversed by horizontal partitions, the *tabulæ* (*tb.*).

In the living animal each pore is the place of origin of a zooid: from the gastropores protrude polypes (Fig. 121, *G*) with hypostome and four knobbed tentacles; from the dactylopores protude long, filamentous, mouthless dactylozooids or feelers (*D*), with irregularly disposed tentacles: the function of these latter is probably protective and tactile, like that of the guard-polypes of Plumularia and the dactylozooids of Hydractinia. The bases of the zooids are connected with a system of delicate tubes, which ramify through the

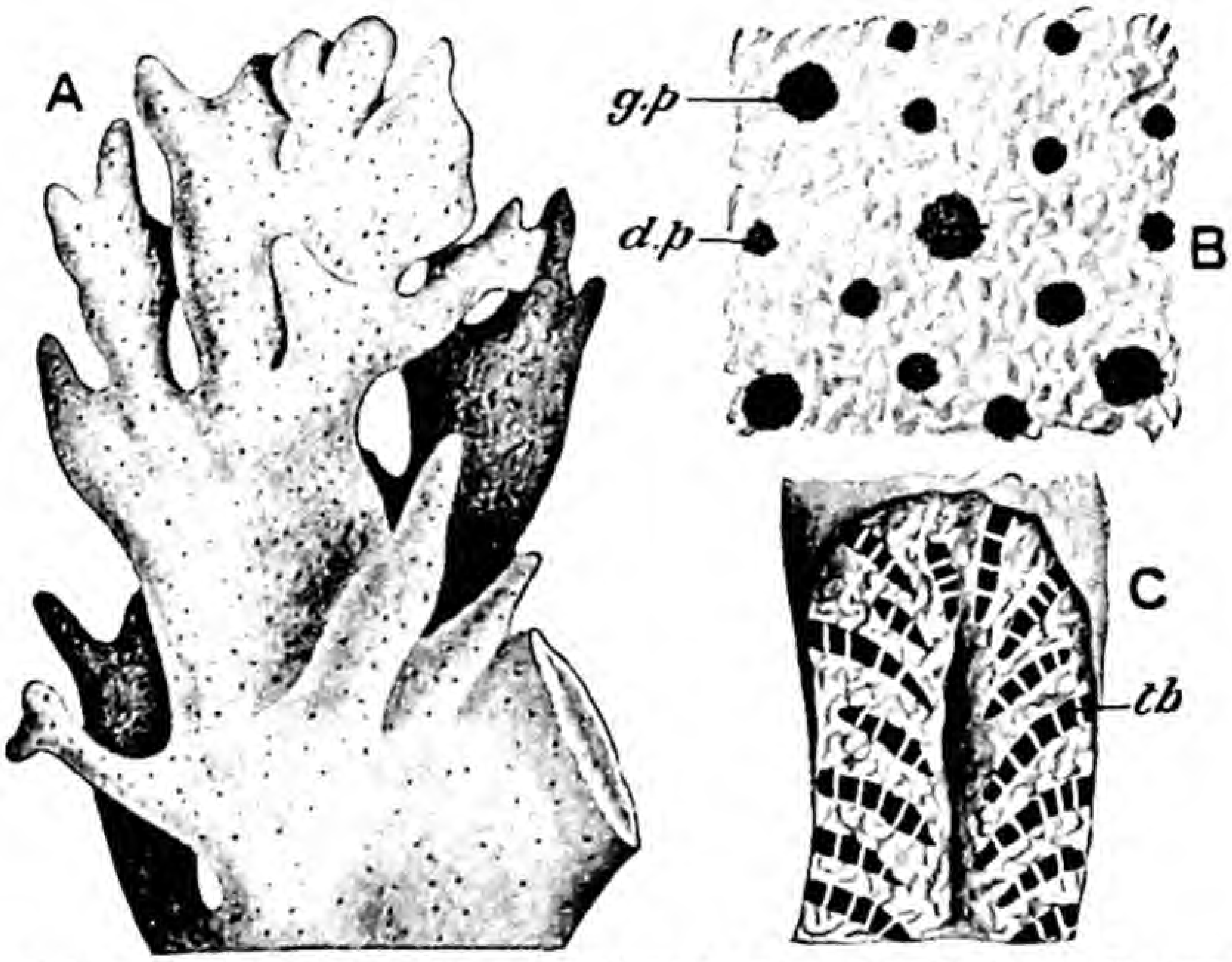


FIG. 120.—**Millepora alcicornis.** *A*, part of skeleton, natural size; *B*, portion of surface, magnified; *C*, vertical section, magnified; *d.p.* dactylopores; *g.p.* gastropores; *tb.* tabulæ. (After Nicholson and Lydekker.)

canals of the coral and represent a much-branched cœnosarc, recalling that of Hydractinia (p. 139).

The cœnosarcal tubes have the usual structure, consisting of ectoderm and endoderm with an intervening mesoglœa. From the relative position of the parts it will be obvious that the calcareous skeleton is in contact throughout with the ectoderm of the colony: it is, in fact, like the horny perisarc of the Hydroidea, a cuticular product of the ectoderm.

The only other genus to which we shall refer is *Stylaster* (Fig. 122), which forms a remarkably elegant tree-like colony, abundantly branched in one plane, and of a deep pink colour. On the branches are little cup-like projections with radiating processes passing from the wall of the cup towards the centre, and

thus closely resembling the true cup-corals belonging to the Actinozoa (*vide* p. 191). But in the case of Stylaster each " cup " is the locus, not of one, but of several zooids—a polype projecting from its centre, and a dactylozooid from

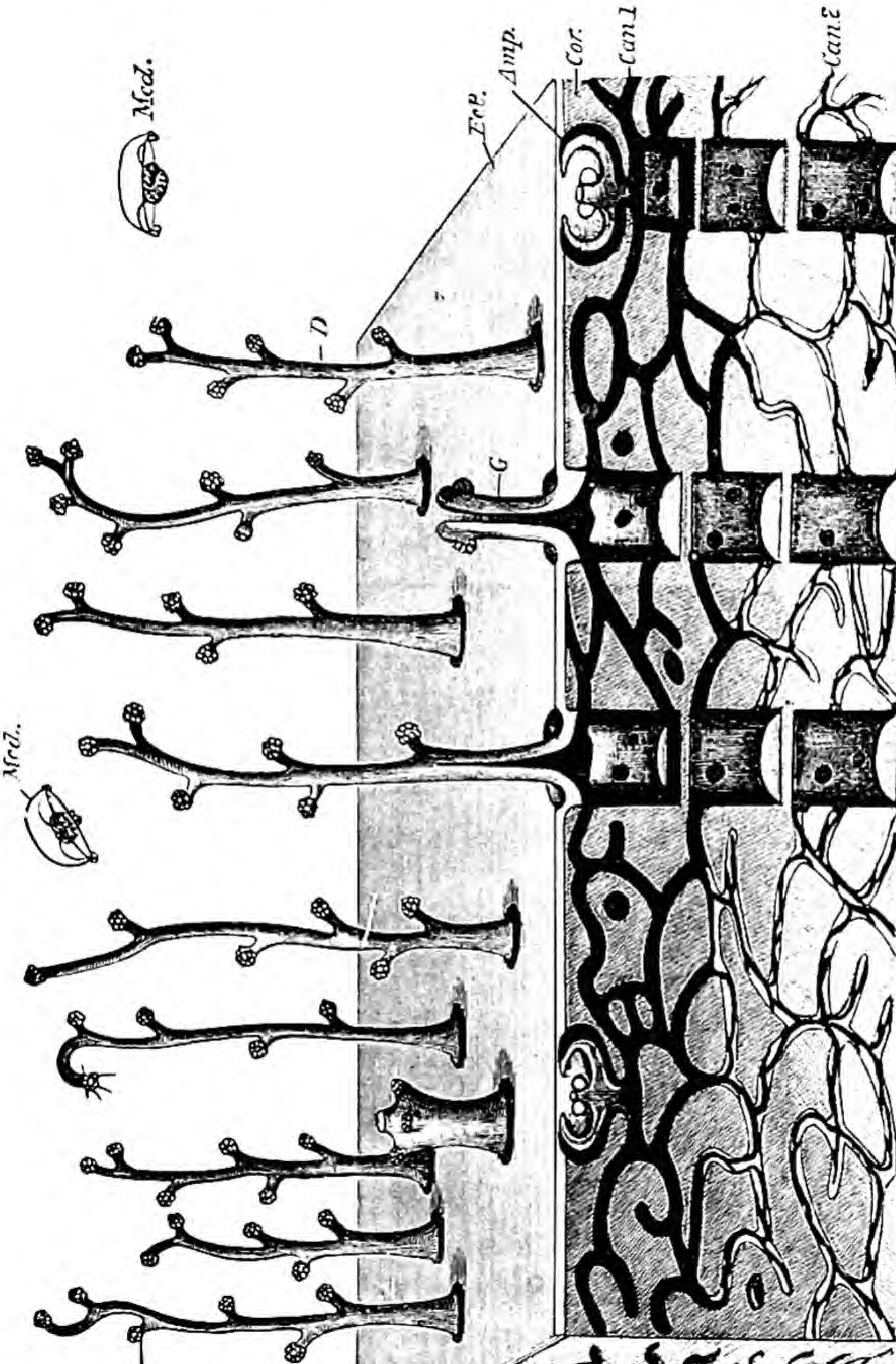


FIG. 121.—Diagrammatic sketch to show the structure of **Millepora**. *Amp.* an ampulla containing a medusa; *Can. 1*, canal system at the surface; *Can. 2*, canal system degenerating in the lower layers of the corallum; *Cor.* corallum; *D*, an expanded dactylozooid with its capitate tentacles; *Ect.* the continuous sheet of ectoderm covering the corallum (*Cor.*); *G.* a gastrozooid, seen in vertical section; *Med.* free-swimming Medusæ; *t.* tentacle; *Tab.* tabula in the pore-tubes. (After Hickson.)

each of the compartments of its peripheral portion. A calcareous projection, the *style*, the presence of which is the origin of the generic name, rises up from the tabula at the bottom of each cup.

The gonophores in most species of Millepora are developed in certain of the pores in dilatations or *ampullæ*; in one species they are developed at the apices of the dactylozooids. They are medusæ, but never have the complete medusa-form, being devoid of velum, mouth, radial canals and tentacles. Both male and female medusæ become free, but the period of free existence is very short.

In Stylaster the medusoid character is much more completely lost, and the gonophores are more of the nature of sporosacs or degraded reproductive zooids lodged in special chambers (*a*) of the coral.

The Hydrocorallina occur only in the tropical portions of the Pacific and

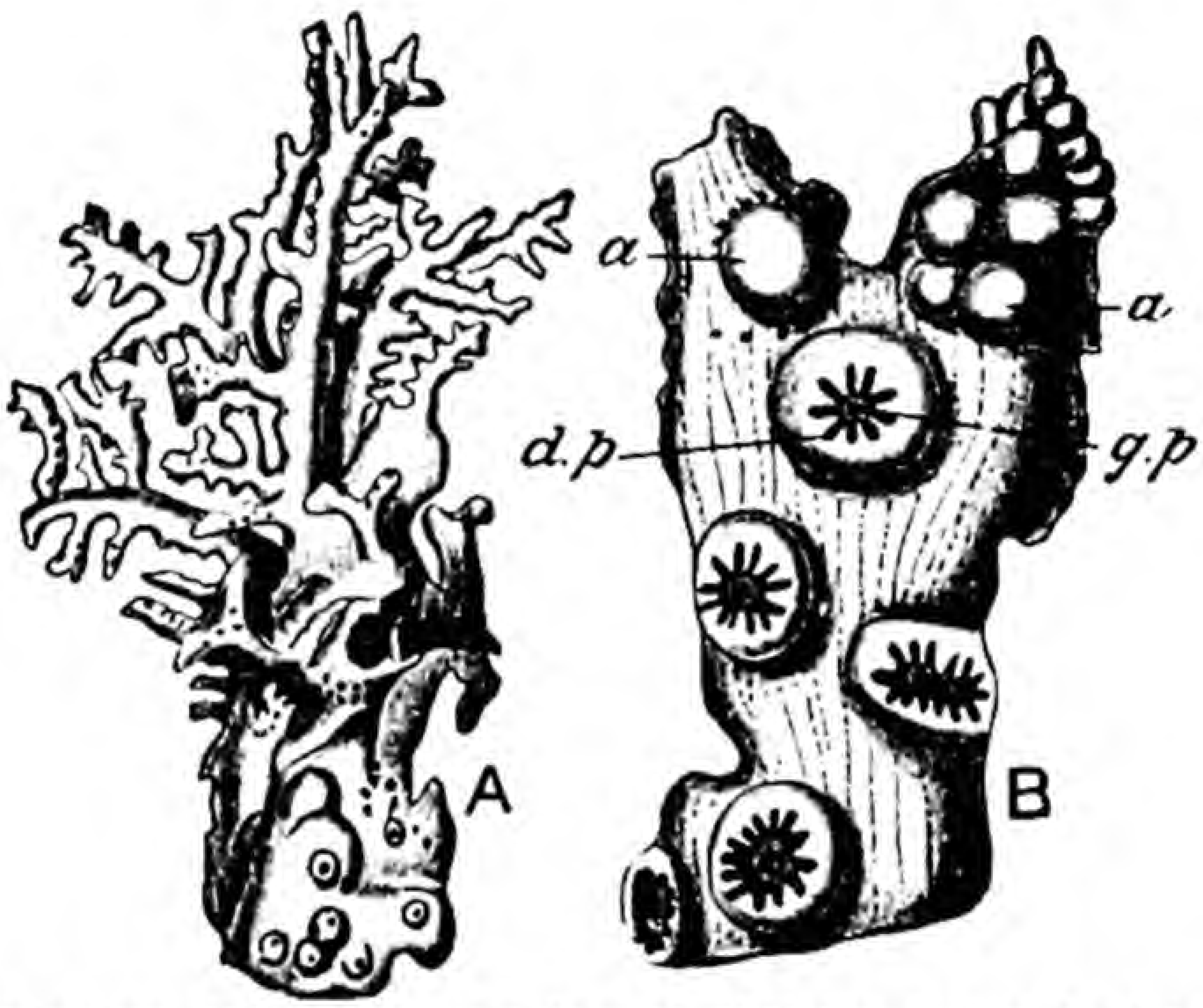


FIG. 122.—**Stylaster sanguineus.** *A*, portion of skeleton natural size; *B*, small portion, magnified; *a*. ampullæ; *d.p.* dactylopores; *g.p.* gastropores. (After Nicholson and Lydekker.)

Indian Oceans, where they are found on the coral-reefs partly or entirely surrounding many of the islands in those seas. Fossil forms are found as far back as the Triassic epoch.

ORDER 4.—SIPHONOPHORA.

The diversity of form exhibited by the members of this order is so great that anything like a general account of it would only be confusing to the beginner, and the most satisfactory method of presentation will be by the study of a few typical genera.

Halistemma (Fig. 123, *A*) occurs in the Mediterranean and other seas, and consists of a long, slender, floating stem, to which a number of structures, differing greatly in form, are attached. At one—the uppermost—end of the stem is an ovoid, bubble-like body containing air—the *float* or *pneumatophore* (*pn.*). Next come a number of closely set, transparent structures (*nct.*), having the

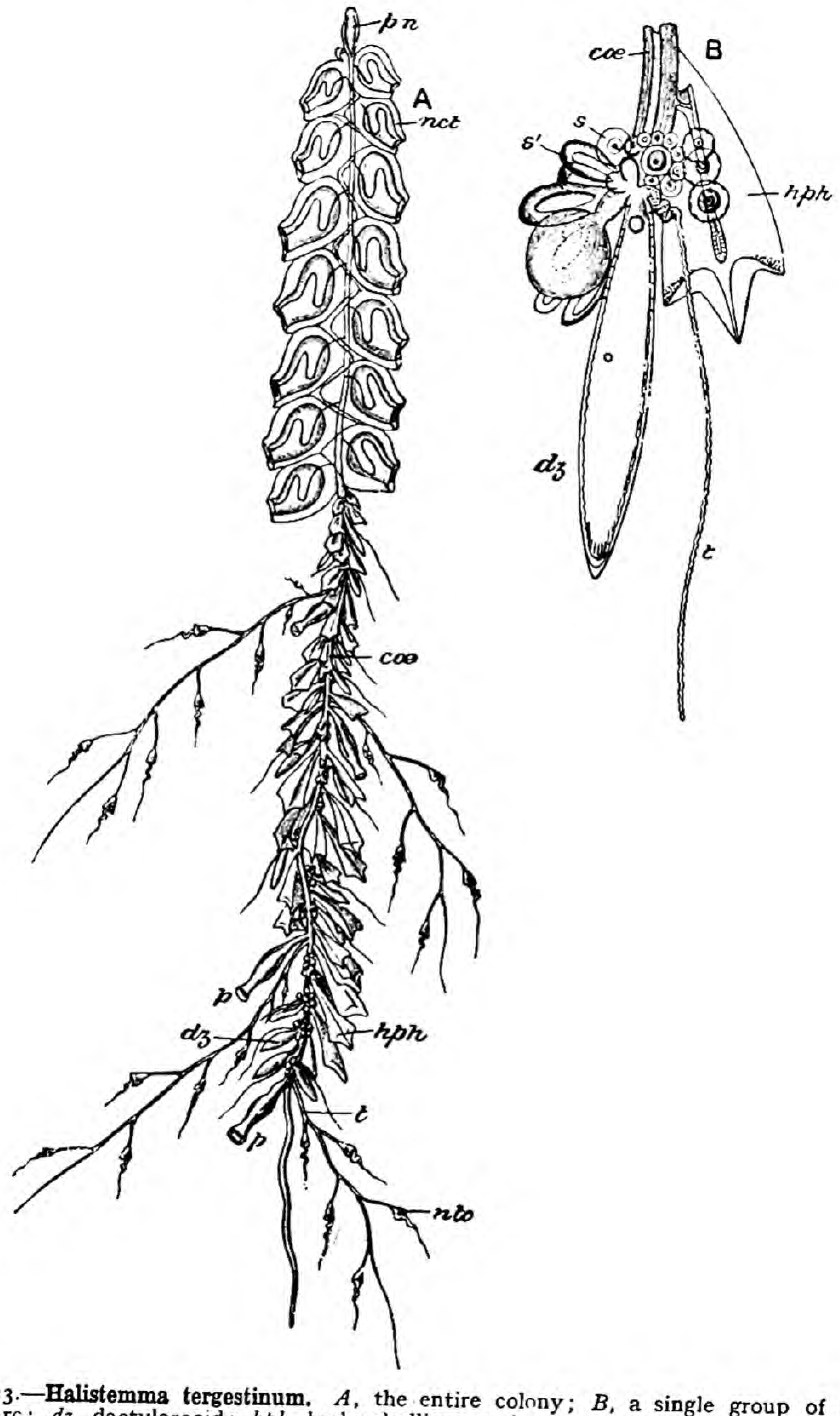


FIG. 123.—**Halistemma tergestinum.** *A*, the entire colony; *B*, a single group of zooids. *cœ*. cœnosarc; *dz*. dactylozooid; *hph*. hydrophyllium or bract; *nct*. nectocalyx or swimming-bell; *ntc*. battery of nematocysts; *p*. polype; *pn*. pneumatophore or float; *s*., *s'*. sporocysts; *t*. tentacle. (After Claus.)

general characters of unsymmetrical medusæ without manubria, each being a deep, bell-like body, with a velum and radiating canals. During life these *swimming-bells* or *nectocalyces* contract rhythmically—*i.e.*, at regular intervals—drawing water into their cavities, and immediately pumping it out, thus serving to propel the entire organism through the water. Below the last nectocalyx the character of the structures borne by the stem changes completely: they are of several kinds, and are arranged in groups which follow one another at regular intervals, and thus divide the stem into segments, like the nodes and internodes of a plant.

Springing from certain of the "nodes" are unmistakable polypes (*p.*), differing, however, from those we have hitherto met with in having no circlet of tentacles round the mouth, but a single long branched tentacle (*t.*) arising from the proximal end, and bearing numerous groups or "batteries" of stinging-capsules (*ntc.*). In the remaining nodes the place of the polypes is taken by dactylozooids or feelers (*dz.*)—mouthless polypes, each with an unbranched tentacle springing from its base. Near the bases of the polypes and dactylozooids spring groups of sporosacs (*B*, *s*, *s'*), some male, others female; and finally delicate, leaf-like, transparent bodies—the *bracts* or *hydrophyllia* (*hph.*)—spring from the "internodes" and partly cover the sporosacs.

It is obvious that on the analogy of such a hydroid polype as Obelia, Halistemma is to be looked upon as a polymorphic floating colony, the stem representing a cœnosarc, and the various structures attached to it zooids—the polypes nutritive zooids, the feelers tactile zooids, the sporosacs reproductive zooids, the bracts protective zooids, and the swimming-bells locomotory zooids. The float may be looked upon as the dilated end of the stem, which has become invaginated or turned in so as to form a bladder filled with air, its outer and inner surfaces being furnished by ectoderm, and the middle portion of its wall by two layers of endoderm, between which the enteric cavity originally extended (Fig. 124, *pn.*). The upper or float-bearing end is proximal—*i.e.*, answers to the attached end of an Obelia-stem: it is the opposite or distal end which grows and forms new zooids by budding.

In some Siphonophora the bracts contain indications of radial canals, so that these structures, as well as the swimming-bells and sporosacs, are formed on the medusa-type, while the hydranths and feelers are constructed on the polype-type.

It will be noticed that the radial symmetry, so characteristic of most of the Hydrozoa previously studied, gives way, in the case of Halistemma, to a bilateral symmetry. The swimming-bells are placed obliquely, and the mouth of the bell is not at right angles to the long axis, so that only one plane can be taken dividing these structures into two equal halves: the same applies to the polype and feelers with their single basal tentacle. When first formed the various

zooids are all on one side of the stem, but the latter becomes spirally twisted during growth, and so causes them to rise irregularly.

The egg of Halistemma gives rise to a ciliated planula resembling that of the other Hydrozoa. At one pole the ectoderm becomes invaginated to form the float (Fig. 125, *pn.*), the opposite extremity is gradually converted into the first

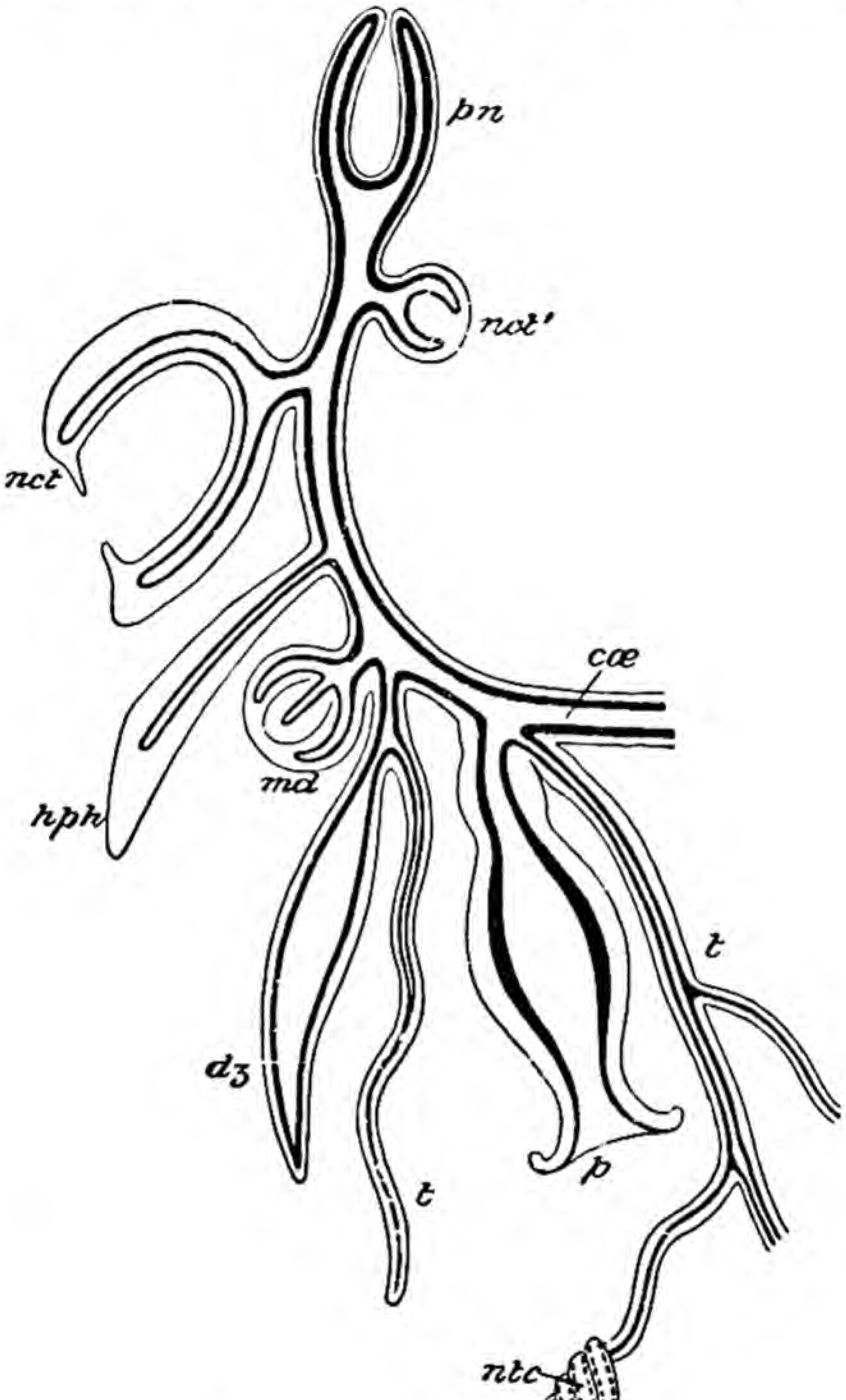


FIG. 124.—Diagram of a **Siphonophore :** the thick line represents endoderm ; the space external to it, ectoderm ; the internal space, the enteric cavity. *cœ.* cœnosarc ; *dz.* dactylozooid ; *hph.* hydrophyllium ; *md.* sporosac ; *ncl. ncl'.* nectocalyces ; *ntc.* battery of nematocysts ; *p.* polype ; *pn.* pneumatophore ; *t.* tentacle. (After Claus.)

polype and a bud appears on one side which becomes the first tentacle (*ten.*). By gradual elongation, and the formation of new zooids as lateral buds, the adult form is produced ; the various zooids are all formed between the first polype and the float, so that the two become further and further apart, being always situated at the distal and proximal ends of the colony respectively.

In an allied form (*Agalma*) the first structure to appear in the embryo is not the float, but the first bract, which grows considerably and envelops the growing embryo in much the same way as the umbrella of a medusa envelops the manubrium. On this and other grounds some zoologists look upon the Siphonophore-colony as a medusa the manubrium of which has extended immensely and produced lateral buds after the manner of some Anthomedusæ (Fig. 108, 7 *a*). On this theory the entire cœnosarc is an extended manubrium and the first or primary bract is the umbrella. But frequently—as in Halistemma—a primary bract is not formed, and when present there appears to be no reason against regarding it as a lateral bud of the axis, of quite the same nature as the remaining zooids.

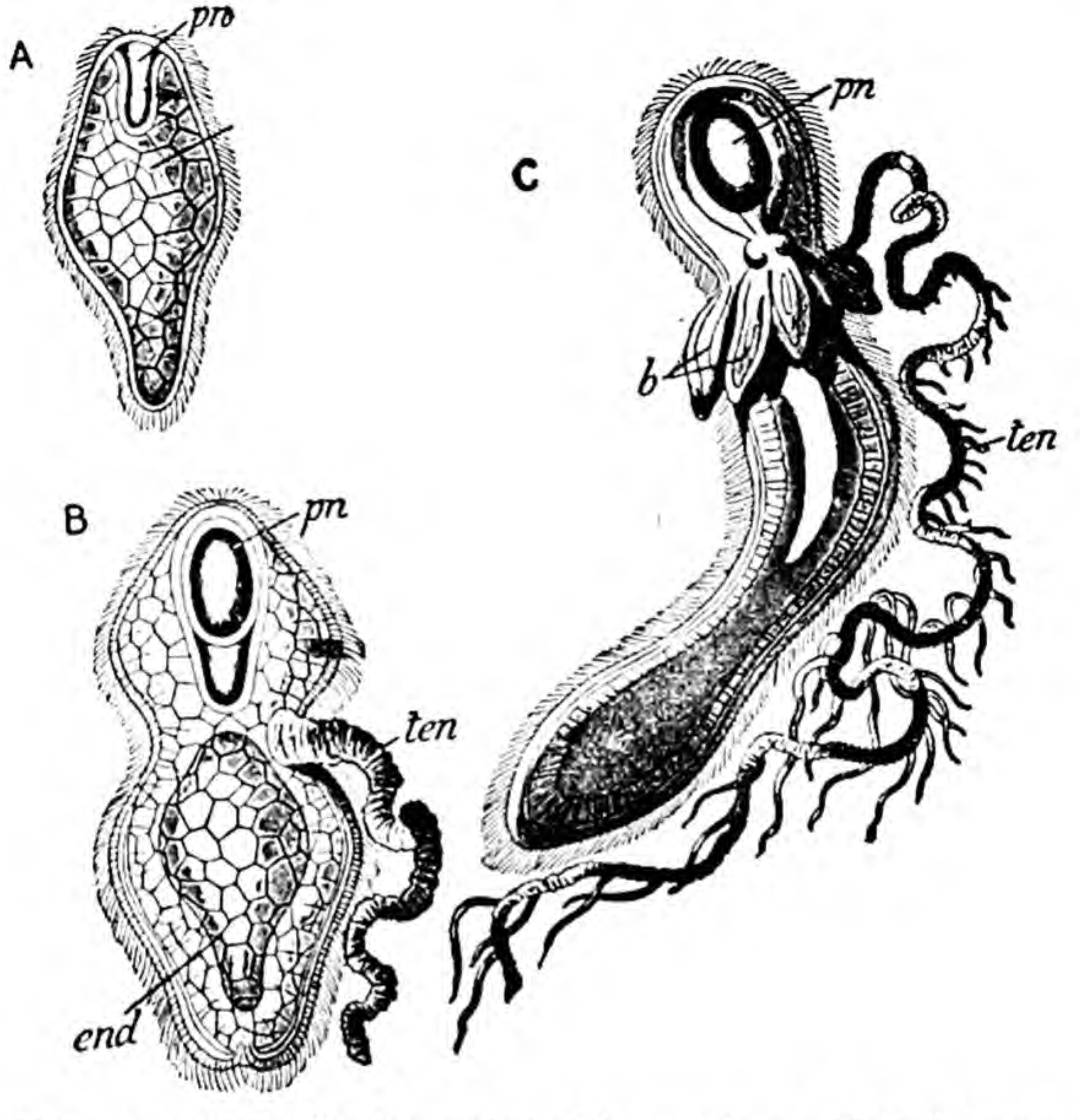


FIG. 125.—Three stages in the development of a **Siphonophore.** (*Cystalia monogastrica.*) *A*, planula with float, an open invagination of the aboral ectoderm; *B*, older larva, a single long tentacle formed; *C*, still older larva in which the definite endoderm is formed, and in which buds of other zooids have been formed; *b.* buds; *end.* endoderm; *pn.* float; *ten.* tentacle. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Haeckel.)

In the well-known "Portuguese man-of-war" (*Physalia*) there is a great increase in proportional size of the float and a corresponding reduction of the rest of the cœnosarc. The float (Fig. 126, *pn.*) has the form of an elongated bladder, from 3 to 12 cm. long, pointed at both ends, and produced along its upper edge into a crest or sail (*cr.*): as a rule it is of a brilliant peacock-blue colour, but orange-coloured specimens are sometimes met with. At one end is a minute aperture communicating with the exterior. There are no swimming-bells, but from the underside of the float hang gastrozooids (*p.*), dactylozooids,

branching blastostyles (*gonodendra*) with groups of medusoids looking like bunches of grapes of a deep blue colour, and long retractile tentacles (*t.*), sometimes several feet in length and containing batteries of stinging-capsules powerful enough to sting the hand as severely as a nettle. The male reproduc-

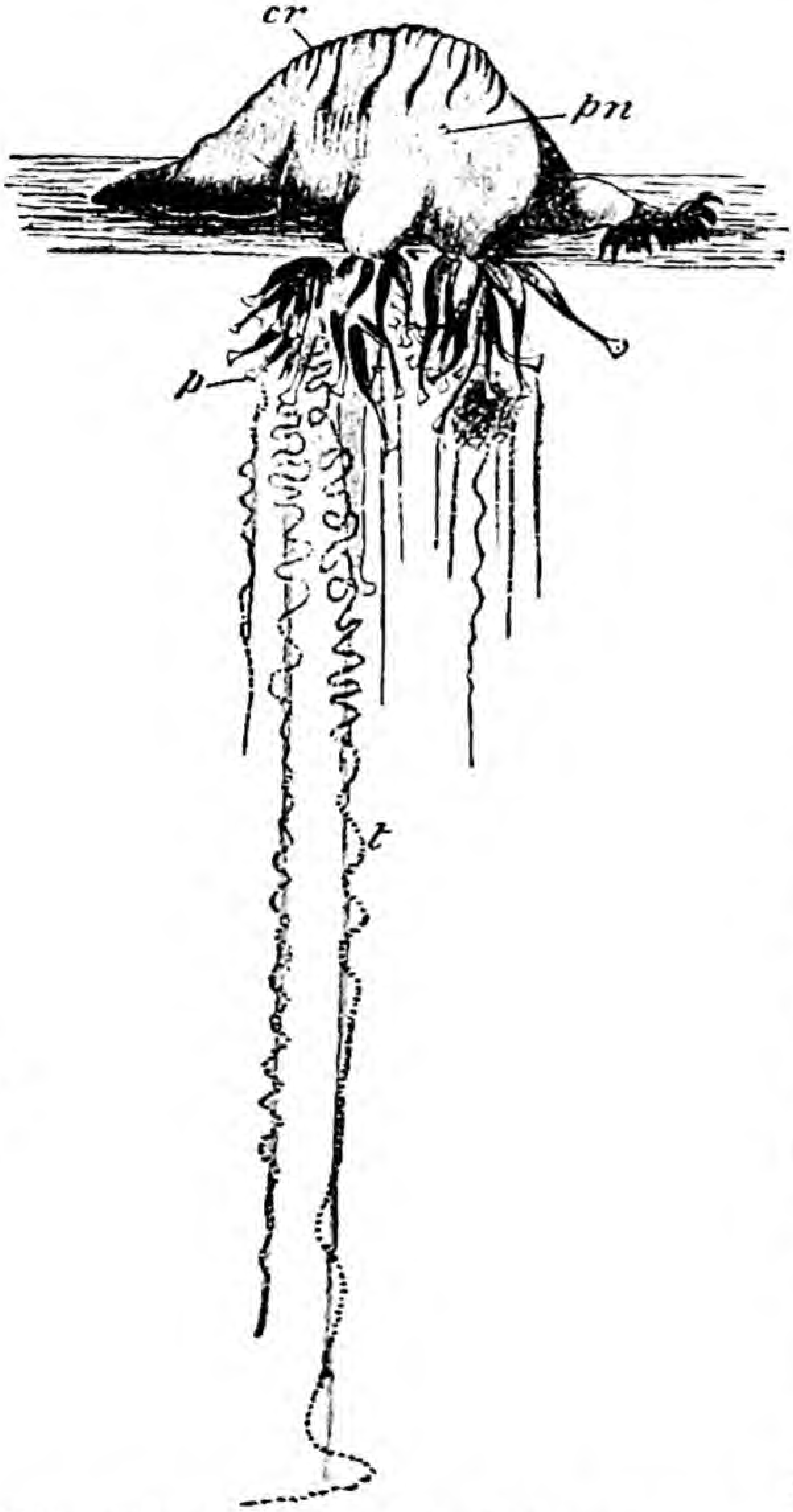


FIG. 126.—**Physalia**: the living animal floating on the surface of the sea. *cr.* crest; *p.* polype; *pn.* pneumatophore; *t.* tentacle. (After Huxley.)

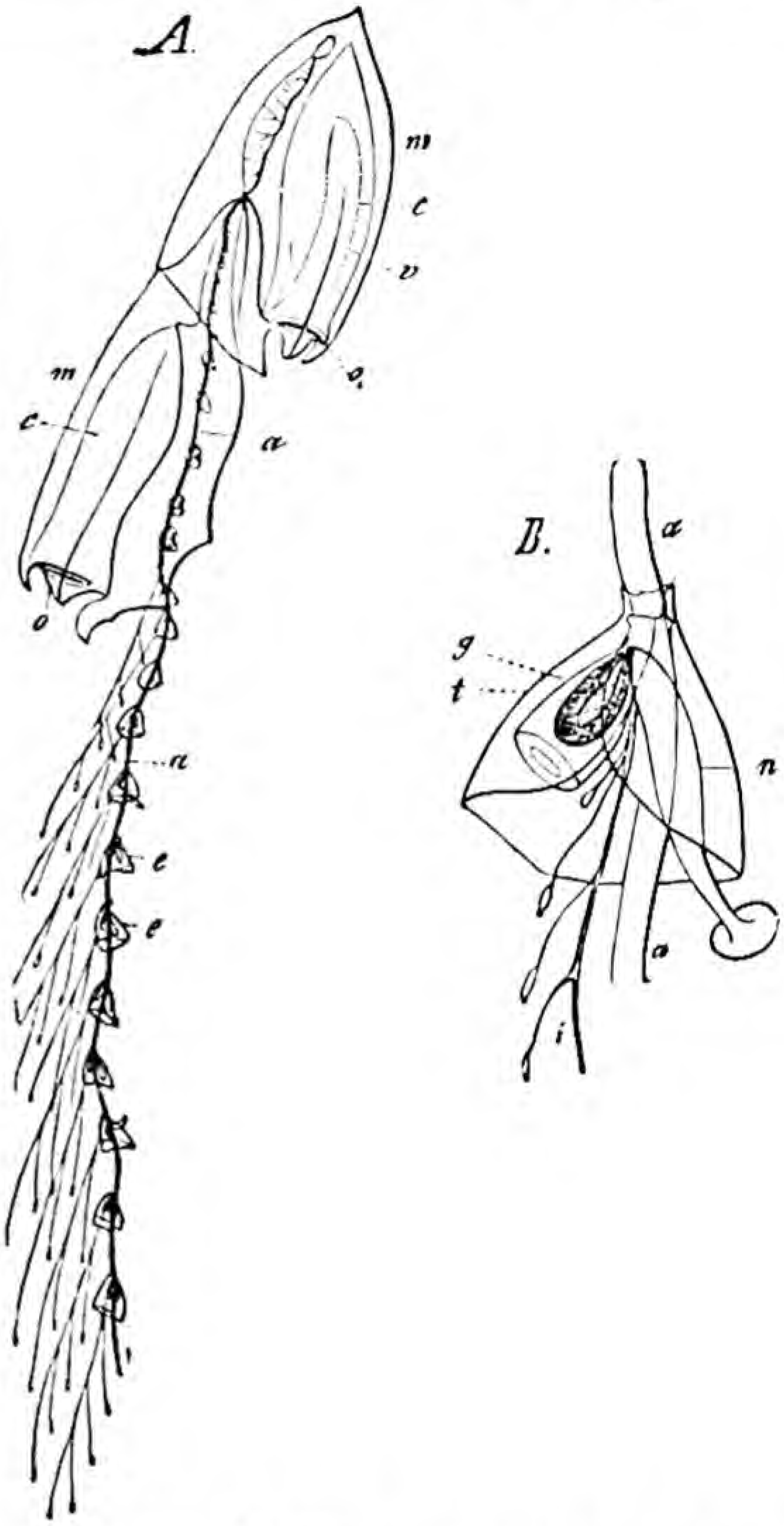


FIG. 127.—**Diphyes campanulata.** *A*, the entire colony; *B*, single group of zooids. *a.* cœnosarc; *c.* cavity of swimming-bell; *e*, groups of zooids; *g*, medusoid; *i*, grappling-line or tentacle; *m*, swimming-bell; *n*, polype; *o*, mouth of swimming-bell; *t*, bract. (From Parker's *Biology*, after Gegenbaur.)

tive zooid remains attached, as in Halistemma, but the female apparently becomes detached as a free medusa.

In *Diphyes* the float is absent. Two swimming-bells (Fig. 127, *A*, *m*) of proportionally immense size are situated at the proximal end of the cœnosarc, and are followed by widely-separated groups of zooids (*B*), each group containing a polype (*n*) with its tentacles (*i*), a medusoid (*g*), and a large enveloping

bract (*t*). The stem often breaks at the internodes, and the detached groups of zooids then swim about like independent organisms.

Porpita is formed on a different type, and has a close general resemblance to a medusa. It consists (Fig. 128) of a discoid body, enclosing a chambered chitinoid shell (*sh.*) containing air, and obviously corresponding with the float of Physalia: each of the chambers communicates with the exterior by a couple of pores. The edge of the disc is beset with long dactylozooids (*t*), and from its lower surface depend numerous closely set blastostyles provided with mouths and bearing medusæ, while in the centre is a single large gastrozooid (*hy.*).

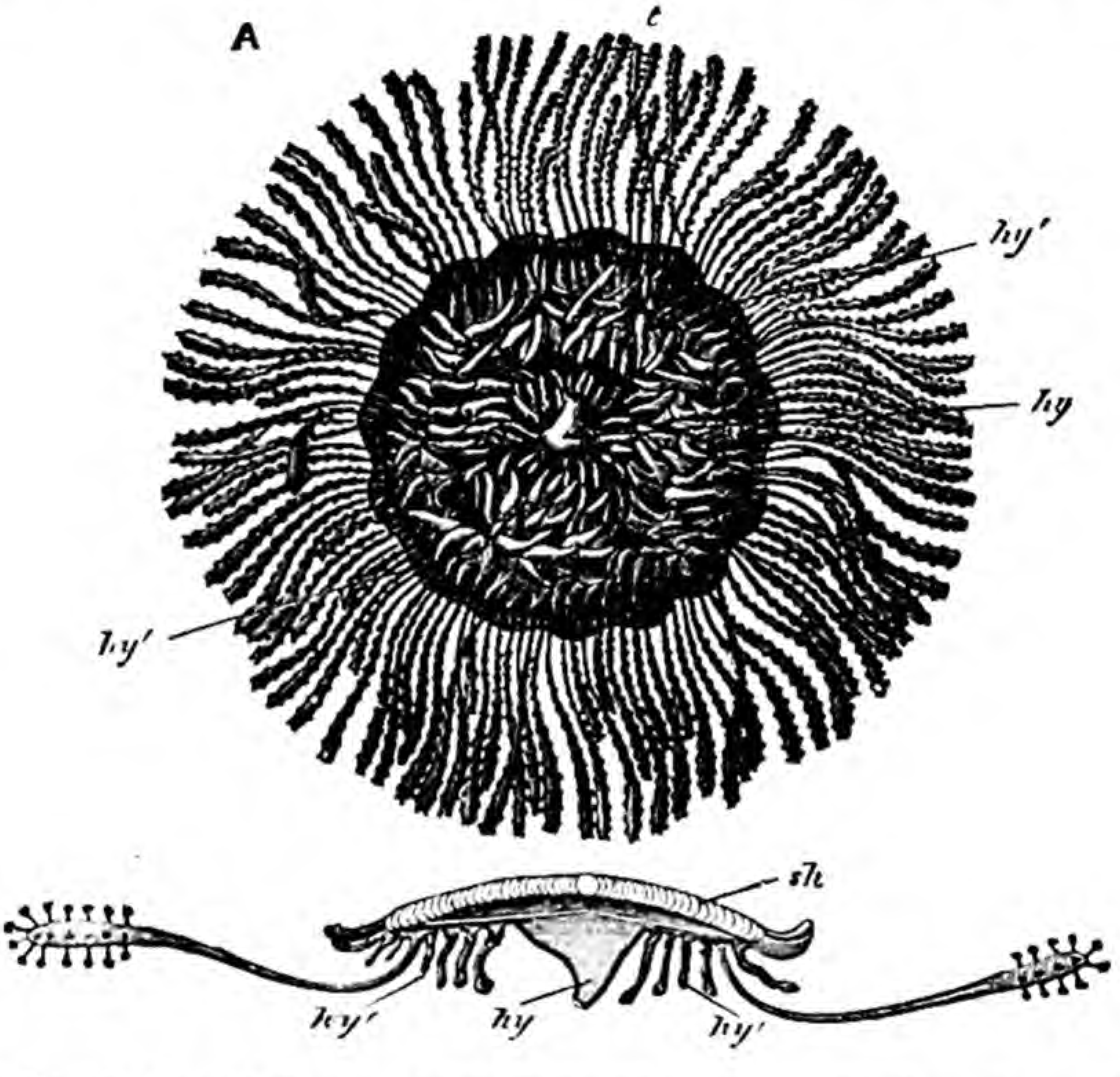


FIG. 128.—**Porpita pacifica.** *A*, from beneath; *B*, vertical section. *hy*, large central gastrozooid; *hy'*, blastostyles; *sh*, chambered shell; *t*, dactylozooids. (From Parker's *Biology*, after Duperry and Koelliker.)

The mouth of the gastrozooid leads into a wide gastric cavity. Between this and the pneumatophore is a thick cellular mass through which ramify numerous canals belonging to two systems. One of these systems is endodermal: it communicates with the endodermal cavities throughout the colony. The other (*tracheal system*) is ectodermal and is lined internally throughout by a chitinous layer; it opens by numerous apertures into the air-chambers of the float. The closely allied genus *Velella* is of rhomboidal form, and bears on its upper surface an oblique sail.

The reproductive zooids are liberated as free medusæ. The eggs give rise to young which have a close resemblance to flat medusæ with manubrium, marginal

tentacles, and an air-chamber or float developed in the ex-umbrella. Thus it is quite possible that the Siphonophora of the Porpita-type may be medusæ, the sub-umbrella of which has given rise to buds forming the feelers and blastostyles. But, as their early development is not known, it is still quite legitimate to describe them in the same terms as the other Siphonophora—*i.e.*, to consider them as hydroid colonies in which the cœnosarc is represented by the discoid or rhomboid body with its contained air-chamber.

ORDER 5.—GRAPTOLITHIDA.

The "Graptolites" are Hydrozoa found in the Upper Cambrian and Silurian rocks. They are known only by their fossilized chitinoid skeleton, all trace of the soft parts having, as in the majority of fossils, disappeared.

With one doubtful exception they are compound, consisting of an elongated tube—the perisarc of the common stem, having attached to it, either in a single or a double row, numerous small projections, the hydrothecæ (Fig. 129, *h.th.*). The cœnosarcal skeleton is strengthened by a slender axis, the *virgula* (*v.*), the proximal end of which is connected with a small dagger-shaped body, the *sicula* (*s.*), supposed to be the skeleton of the primary zooid by the budding of which the colony was produced. In connection with some species oval or cup-like capsules have been found: these may be of the nature of gonothecæ. It is possible that some Graptolites were planctonic organisms having floating organs resembling those of the Siphonophora.

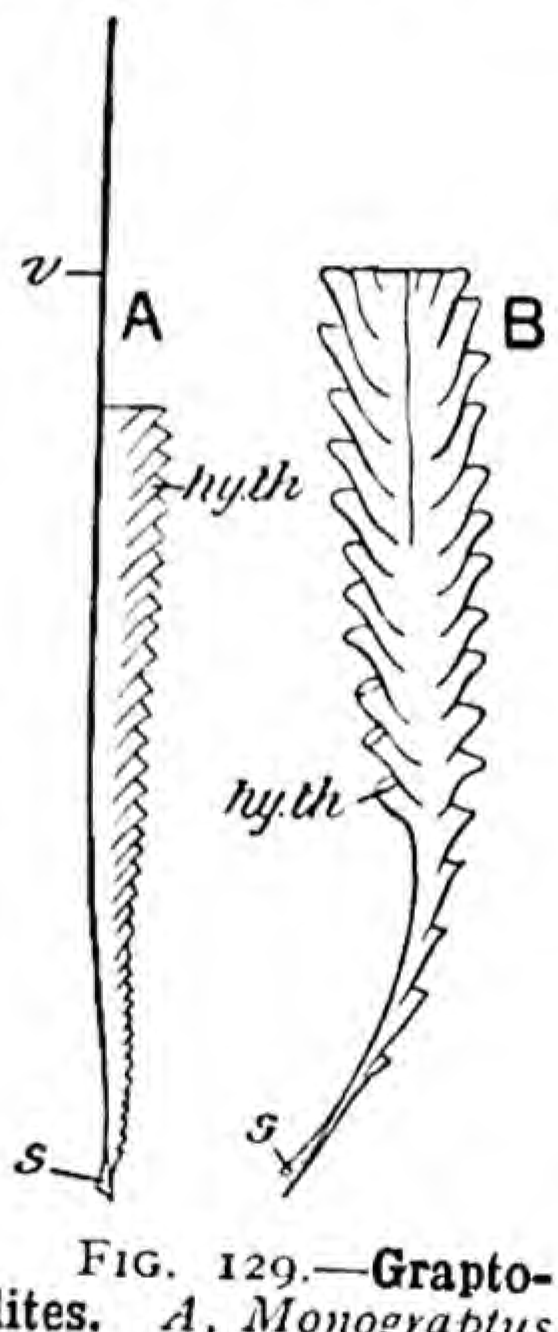


FIG. 129.—**Graptolites.** *A*, *Monograptus colonus*; *B*, *Dimorphograptus*, both magnified. *hy.th.* hydrotheca; *s.* sicula; *v.* virgula. (After Nicholson and Lydekker.)

ORDER 6.—STROMATOPOROIDEA.

The Stromatoporoids are fossil organisms, possibly Hydrozoa which flourished in the Silurian and especially in the Devonian. They built a massive calcareous skeleton of superposed laminæ and vertical pillars, both permeated by minute canals. With Corals, they were the reef-builders of mid-Palæozoic times.

ADDITIONAL REMARKS ON THE HYDROZOA.

The vast majority of Hydrozoa are marine, the only exceptions being *Hydra*, found all over the world; *Cordylophora*, one of the Anthomedusæ, found in Europe, America, Australia, and New Zealand; *Polypodium*, also an Anthomedusa, found in the Volga, where in one stage of its existence it is parasitic on the eggs of the Sturgeon; *Craspedacusta* (*Limnocodium*), a Trachymedusa originally discovered in the Victoria regia tank at the Botanical Gardens Regent's Park (its life-history includes a polype-like stage known under the name *Microhydra*); and *Limnocnida*, found in Lakes Tanganyika and Victoria Nyanza and in the river Niger.

The oldest known Hydrozoa are the Graptolites, found first in the Cambrian rocks; *Hydractinia* occurs in the Cretaceous epoch, and Hydrocorallinæ from the Cretaceous onwards.

Parasitism, although rare, is not unknown in the class. *Polypodium*, one of the Anthomedusæ, is parasitic during part of its existence, in the ovary

of the Sturgeon; and *Cunina*, one of the Narcomedusæ, is parasitic on a Trachymedusa.

In the section on the Protozoa we saw that while the majority of species are independent cells, each performing alone all the essential functions of an animal, others, such as Pandorina, Volvox, and Proterospongia, consist of numerous unicellular zooids associated to form a colony in which a certain division of labour obtains, the function of reproduction, for instance, being assigned to certain definite cells and not performed by all alike. Thus the colonial Protozoa furnish an example of *individuation*, numerous cells combining to form a colony in which the several parts are dependent one upon another, and which may therefore be said to constitute, from the physiological point of view, an individual of a higher order than the cell.

This is still more notably the case in the Parazoa and lower Metazoa, such as Ascetta and Hydra, in which we have numerous cells combined to form a permanent two-layered sac with a terminal aperture, some of the cells having digestive, others tactile, others reproductive functions.

In the Hydrozoa we see this process carried a step further. Budding takes place and colonies are produced, the various zooids of which—each the equivalent of a Hydra—instead of remaining all alike, become differentiated both morphologically and physiologically, so as to differ immensely from one another both in form and function. In Obelia, for instance, reproduction is made over exclusively to the medusæ, while in Halistemma we have zooids specially set apart, not only for reproductive but for tactile and protective purposes. Thus in Halistemma and the other Siphonophora there is a very complete subordination of the individual zooids to the purposes of the colony as a whole, the colony thus assuming, from the physiological point of view, the characteristics of a single individual, and its zooids the character of organs.

CLASS II.—SCYPHOZOA.

1. Example of the Class—The Common Jelly-Fish (*Aurelia aurita*).

Aurelia is the commonest of the larger jelly-fishes, and is often found cast up on the seashore, when it is readily recognizable by its gelatinous, saucer-shaped umbrella, three or four inches in diameter, and by having near the centre four red or purple horseshoe-shaped bodies—the gonads—lying embedded in the jelly.

External Characteristics.—The general arrangement of the parts of the body is very similar to what we are already familiar with in the hydrozoan jelly-fishes. Most conspicuous is the concavo-convex *umbrella*, the convex surface of which—the ex-umbrella—is uppermost in the ordinary swimming position (Figs. 130 and 131, *A*). The outline is approximately circular, but is

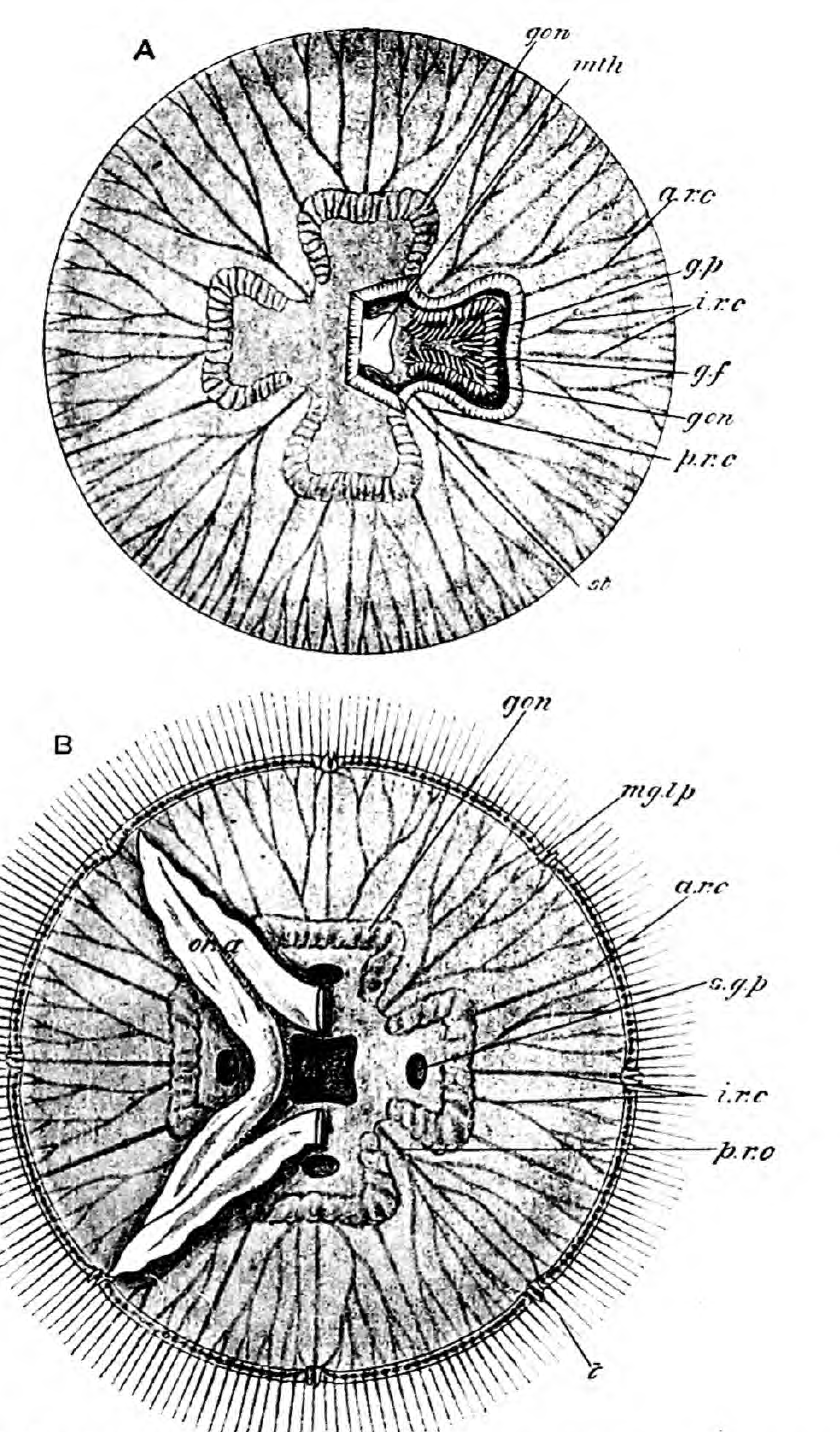


FIG. 130.—**Aurelia aurita.** *A*, dorsal view, part of the ex-umbrella cut away to show part of the stomach and one of the four gastric pouches; *B*, ventral view—two of the oral arms are removed. *a.r. c.* ad-radial canal; *g. f.* gastric filaments; *gon.* gonads; *g. p.* gastric pouch; *i.r. c.* inter-radial canal; *mg. lp.* marginal lappet; *mth.* mouth; *or. a.* oral arm; *p.r. c.* per-radial canal; *s.g. p.* sub-genital pit; *st.* stomach; *t.* tentacles.

broken by eight notches, in each of which lies a pair of delicate processes, the *marginal lappets* (*mg. lp.*) : between the pairs of lappets the edge of the umbrella is fringed by numerous close-set *marginal tentacles* (*t.*).

A narrow region of the umbrella adjoining the edge is very thin and flexible : the structure thus constituted, with its marginal notches and the fringe of marginal tentacles, is the *velarium*. Unlike the true velum of the medusæ of the Hydrozoa the velarium contains endodermal canals.

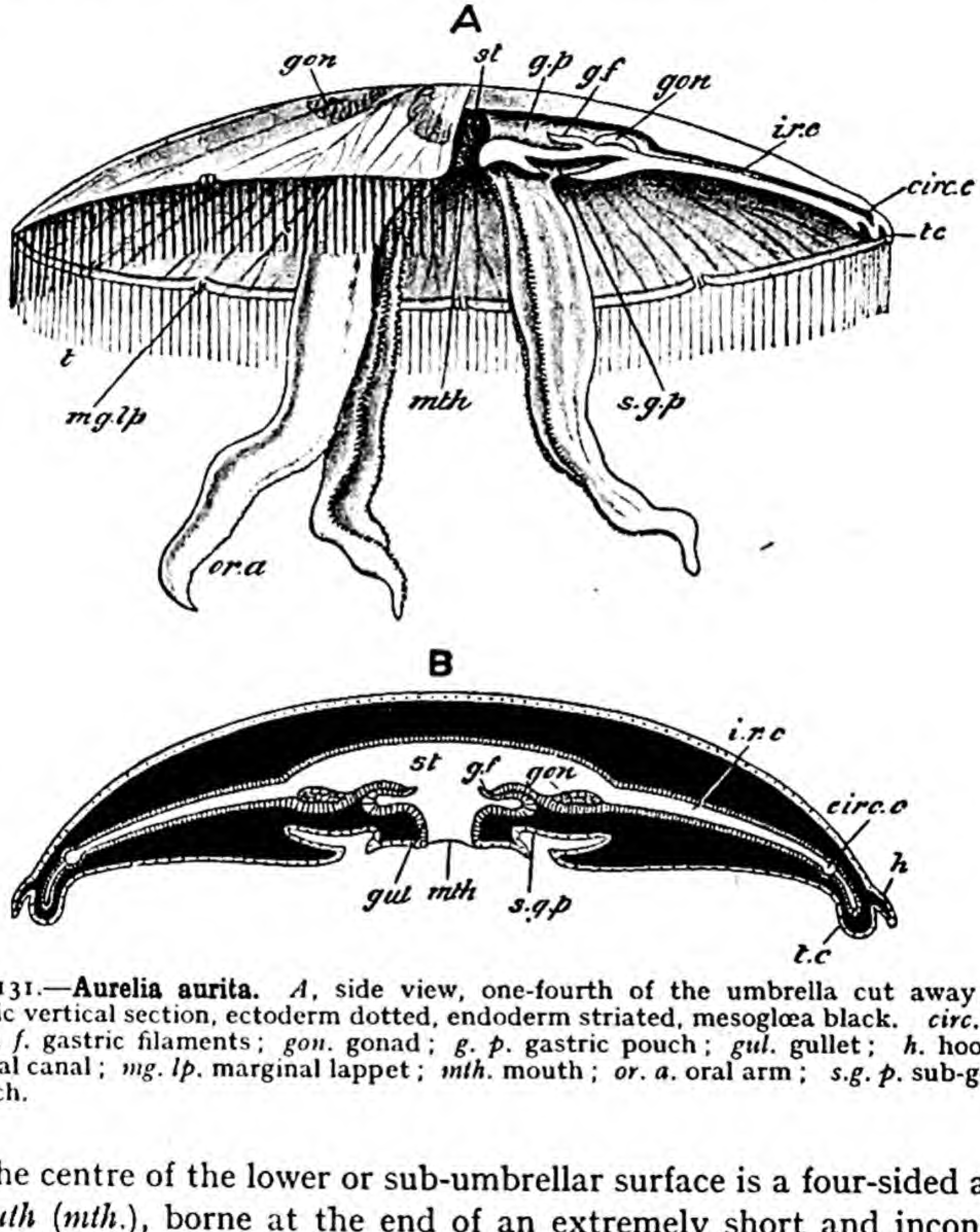


FIG. 131.—**Aurelia aurita.** *A*, side view, one-fourth of the umbrella cut away; *B*, diagrammatic vertical section, ectoderm dotted, endoderm striated, mesoglœa black. *circ. c.* circular canal; *g. f.* gastric filaments; *gon.* gonad; *g. p.* gastric pouch; *gul.* gullet; *h.* hood; *i.r. c.* inter-radial canal; *mg. lp.* marginal lappet; *mth.* mouth; *or. a.* oral arm; *s.g. p.* sub-genital pit; *st.* stomach.

In the centre of the lower or sub-umbrellar surface is a four-sided aperture, the *mouth* (*mth.*), borne at the end of an extremely short and inconspicuous *manubrium*: surrounding it are four long delicate processes, the *oral arms* (*or. a.*), lying one at each angle of the mouth and uniting around it. Each arm consists of a folded membrane, tapering to a point at its distal end, beset along its edges with minute lobules, and abundantly provided with stinging-capsules. The angles of the mouth and the arms lie in the four per-radii, *i.e.*, at the end of

the two principal axes of the radially symmetrical body: of the marginal notches with their lappets, four are per-radial and four inter-radial.

At a short distance from each of the straight sides of the mouth, and therefore inter-radial in position, is a nearly circular aperture leading into a shallow pouch, the *sub-genital pit* (*s.g. p.*), which lies immediately beneath one of the conspicuously coloured gonads (*gon.*). The sub-genital pits have no connection with the reproductive system.

Digestive Cavity and Canal-System.—The mouth leads by a short tube or *gullet* (*gul.*), contained in the manubrium, into a spacious *stomach* (*st.*), which occupies the whole middle region of the umbrella, and is produced into four wide inter-radial *gastric pouches* (*g. p.*), which extend about halfway from the centre to the circumference, and are separated from one another by thick pillar-like portions of the umbrella-jelly. In the outer or peripheral wall of each gastric pouch are three small apertures, leading into as many *radial canals*, which pass to the edge of the umbrella and there unite in a very narrow *circular canal* (*circ. c.*). The canal, which opens by the middle of the three holes, is of course inter-radial (*i.r. c.*): it divides immediately into three, and each division branches again: the canals from the other two holes are ad-radial (*a.r. c.*), and pass to the circular canal without branching. There is also an aperture in the re-entering angle between each two gastric pouches: this leads into a per-radial canal (*p.r. c.*), which, like the inter-radial, branches extensively on its way to the edge of the umbrella.

The general arrangement of the **cell-layers** in Aurelia is the same as in a hydroid medusa (Fig. 131, *B*). The main mass of the umbrella is formed of gelatinous mesoglœa, which, however, is not structureless, but is traversed by branching fibres and contains amœboid cells derived from the endoderm. Both ex- and sub-umbrellæ are covered with ectoderm, and the stomach and canal system are lined with endoderm, which is ciliated throughout.

It was mentioned above that in the free medusa the **gonads** appear through the transparent umbrella as coloured horseshoe-shaped patches. Their precise position is seen by cutting away a portion of the ex-umbrella so as to expose one of the gastric pouches from above (Fig. 130, *A*). It is then seen that the gonad (*gon.*) is a frill-like structure lying on the floor of the pouch and bent in the form of a horseshoe with its concavity looking inwards, *i.e.*, towards the mouth. Being developed from the floor of the enteric cavity, the gonad is obviously an endodermal structure: when mature, its products—ova or sperms—are discharged into the stomach and pass out by the mouth. Here, then, is an important difference from the Hydrozoa, in which the generative products are usually located in the ectoderm, and are always discharged directly on the exterior. The sexes are lodged in distinct individuals.

Lying parallel with the inner or concave border of each gonad is a row of delicate filaments (Figs. 130, 131, *g. f.*), formed of endoderm with a core of

mesoglœa and abundantly supplied with stinging-capsules. These are the **gastric filaments** or **phacellæ**: their function is to kill or paralyse the prey taken alive into the stomach. No such endodermal tentacles are known in the Hydrozoa.

Muscular and Nervous Systems.—The contractions of the bell by which the animal is propelled through the water are effected by means of a muscular zone round the edge of the sub-umbrella. The nervous system is formed on a different plan from that of the hydroid medusæ. Extending over the sub-umbrellar surface between the superficial epithelial layer of ectoderm and the muscular layer is a plexus of simple nerve-fibres. This presents radial thickenings, most strongly developed externally in the per-radii and inter-radii, corresponding to the position of the marginal notches and sense-organs. About the base of each of the latter are special groups of nerve-cells. A slight ring-like thickening of

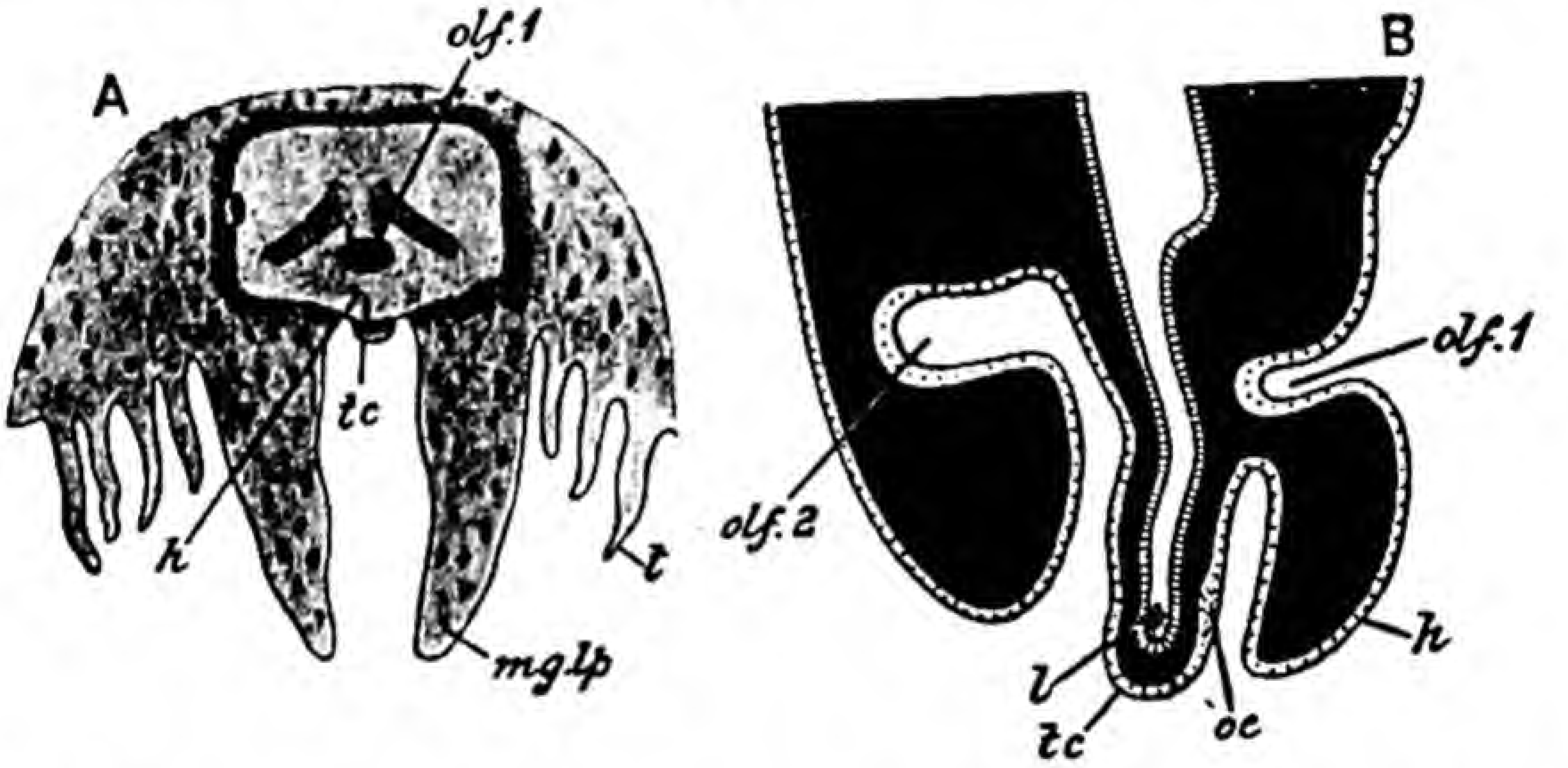


FIG. 132.—**Aurelia aurita.** *A*, small portion of edge of umbrella, showing the relations of the tentaculocyst; *B*, vertical section of the same region (diagrammatic). *h.* hood; *l.* calcareous concretion; *mg. lp.* marginal lappet; *oc.* ocellus; *olf. 1*, *olf. 2*, olfactory pits. (Altered from Lankester.)

the plexus extends round the margin in the neighbourhood of the marginal canal.

The **sense-organs** (Fig. 132) are lodged in the marginal notches in close relation with the nerve-patches: like the latter, therefore, four of them are per-radial and four inter-radial. Each consists of a peculiar form of sense-club or *tentaculocyst*, containing a prolongation of the circular canal, and thus representing a hollow instead of a solid tentacle. At the extremity are calcareous concretions (*l.*) derived from the endoderm, and on the outer side is an ectodermal pigment-spot or *ocellus* (*oc.*). The tentaculocysts are largely hidden by the marginal lappets (*mg. lp.*) and by a hood-like process (*h.*) connecting them. Their function has been shown to be the initiation and control of the rhythmic swimming movements of the animal. After removal of all tentaculocysts, the animal no longer exhibits spontaneous movements; removal of part of these organs reduces the frequency of the rhythmic contractions of the bell. In connection with each tentaculocyst are two depressions, one on the ex-umbrella

(*olf. 1*), the other immediately internal to the sense-club (*olf. 2*) : these depressions are lined with sensory epithelium and are called *olfactory pits*.

The **development** and **life-history** of Aurelia present several striking and characteristic features. The fertilized ovum divides regularly and forms a morula, which, by accumulation of fluid in its interior, becomes a blastula—a closed sac with walls formed of a single layer of cells. One end of this sac becomes invaginated to form the gastrula. The blastopore or gastrula-mouth

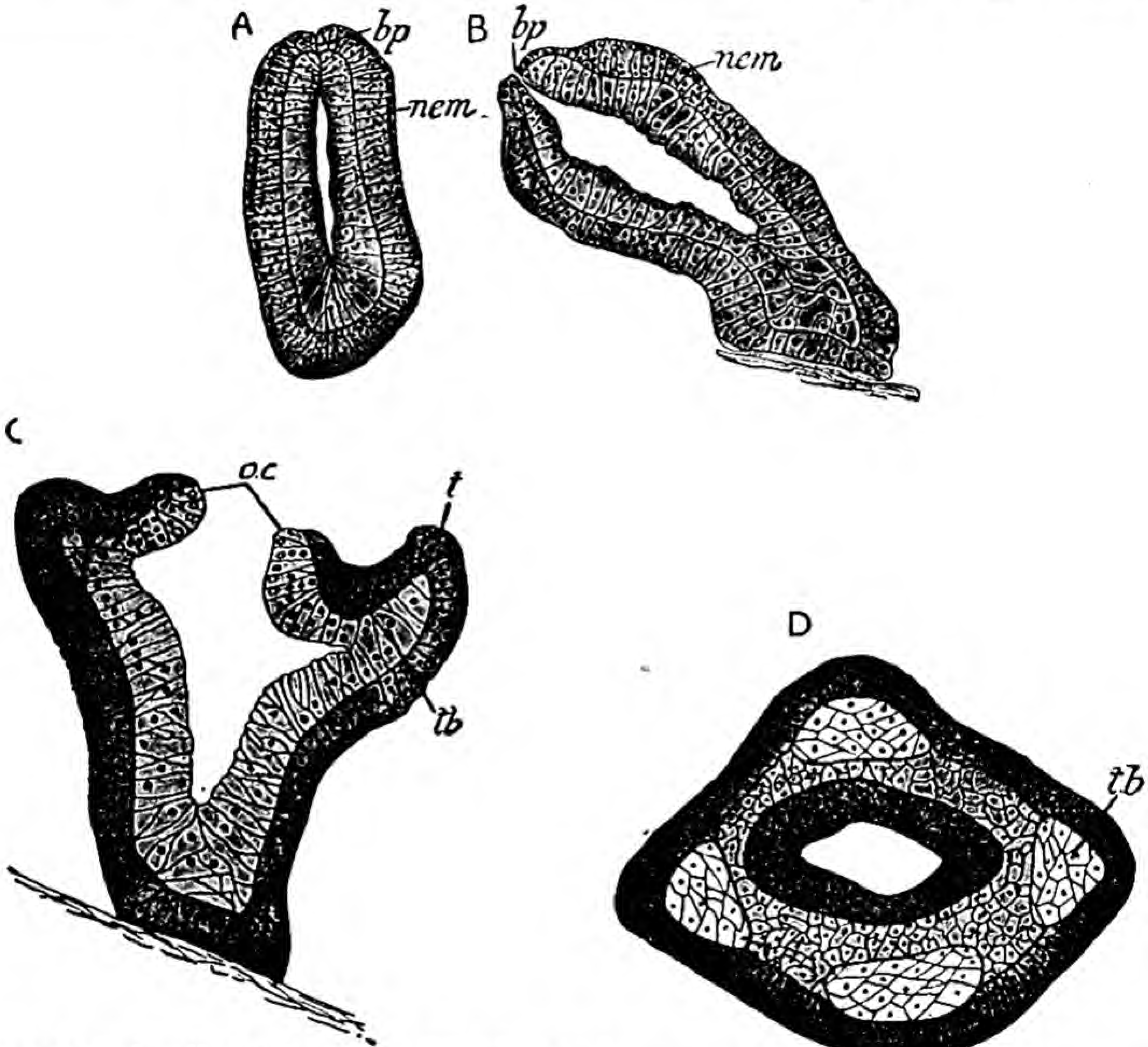


FIG. 133.—**Aurelia aurita,** development. *A*, free-swimming planula ; *B*, stage just after fixation ; *C*, longitudinal section and *D*, transverse section through a specimen with four tentacles ; *bp*. blastopore reduced to a mere slit ; *nem*. nematocysts ; *o. c.* oral cone ; *t*. tentacle ; *t. b.* tentacle basis of vacuolated endoderm. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Hein.)

does not completely close, the resulting two layered *planula* (Fig. 133, A) differing in this respect, as well as in its mode of formation, from the corresponding stage of a Hydrozoon.

The planula swims about by means of the cilia with which its ectodermal cells are provided, and, after a brief free existence, settles down, loses its cilia, and becomes attached by one pole (*A*, *B*). At the opposite pole the definite mouth is formed (*C*). On two opposite sides of the mouth hollow processes

grow out, forming the first two tentacles: soon two others appear at right angles to these, the organism thus being provided with four per-radial tentacles. Subsequently four inter-radial and eight ad-radial tentacles appear. At the same time the attached or proximal end is narrowed into a stalk-like organ of attachment (Fig. 134, *A*) and the endoderm of the enteric cavity is produced into four longitudinal ridges, inter-radial in position, and distinguished as the

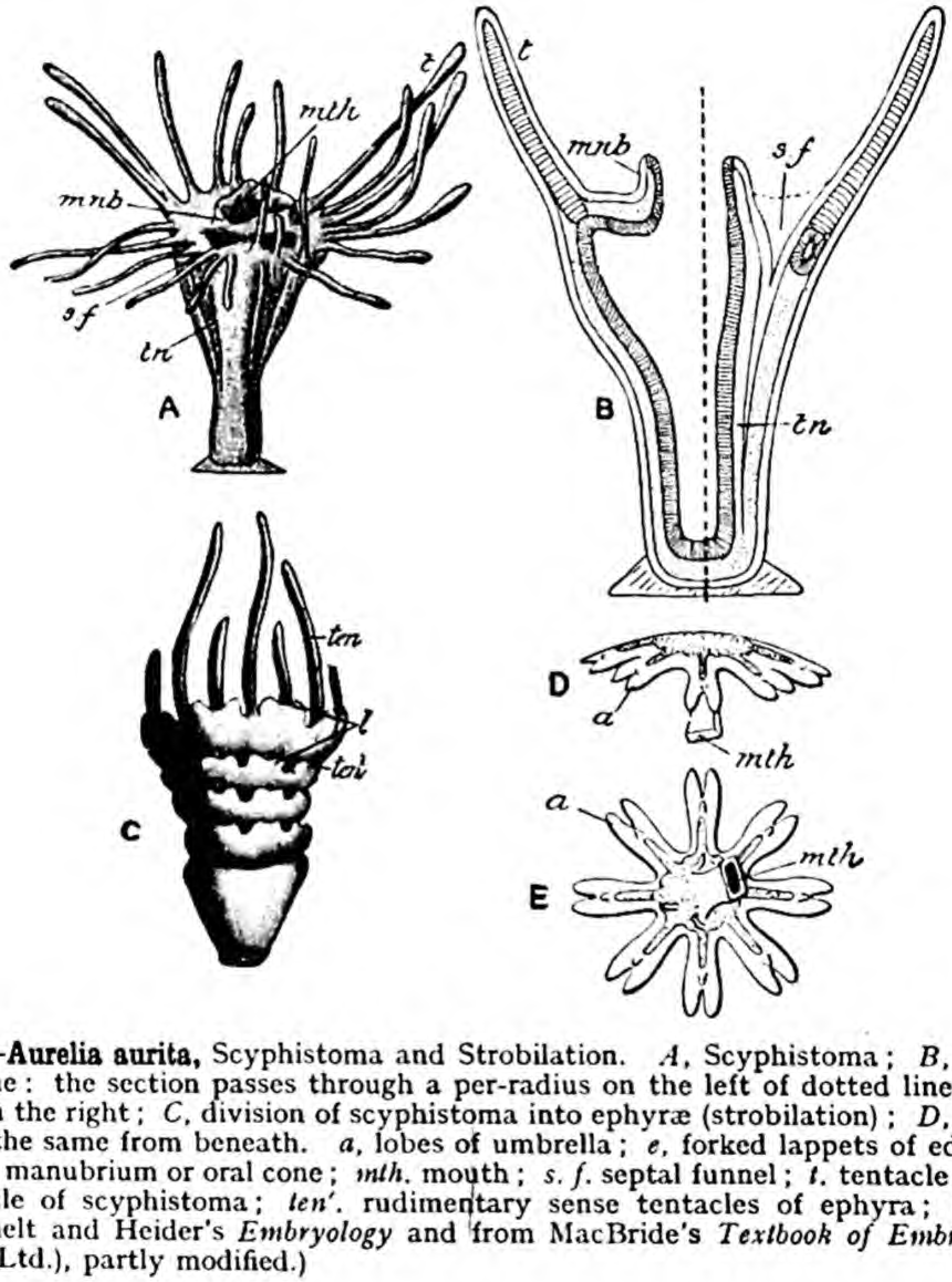


FIG. 134.—**Aurelia aurita,** Scyphistoma and Strobilation. *A*, Scyphistoma; *B*, longitudinal section of same: the section passes through a per-radius on the left of dotted line, through an inter-radius on the right; *C*, division of scyphistoma into ephyræ (strobilation); *D*, ephyra from the side; *E*, the same from beneath. *a*, lobes of umbrella; *e*, forked lappets of edge of disc of ephyra; *mnb*. manubrium or oral cone; *mth*. mouth; *s. f.* septal funnel; *t*. tentacle; *ten*. degenerating tentacle of scyphistoma; *ten'*. rudimentary sense tentacles of ephyra; *tn*. tænioles. (From Korschelt and Heider's *Embryology* and from MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), partly modified.)

gastric ridges or *tænioles*. The mouth (*A*, *mth*.) assumes a square outline, and its edges become raised so as to form a short manubrium (*mnb*.); and, finally, the ectoderm of the distal surface—*i.e.*, the region lying between the mouth and the circlet of tentacles—becomes invaginated in each inter-radius so as to produce four narrow funnel-like depressions—the *septal funnels* or *infundibula* (*A* and *B*, *s. f.*)—sunk in the four gastric ridges.

The outcome of all these changes is the metamorphosis of the planula into a polype (*A*), not unlike a Hydra or the hydrula-stage of the Hydroidea, but distinguished by a pronounced differentiation of structure, indicated by the sixteen tentacles developed in regular order, and the four gastric ridges with their septal funnels. The Scyphozoon-polype is called a *scyphistoma*.

The scyphistoma may grow to a height of half an inch, and sometimes multiplies by budding. After a time it undergoes a process of transverse fission or strobilation (*C*), becoming divided by a series of constrictions which deepen until the polype assumes the appearance of a pile of saucers, each with its edge produced into eight bifid lobes, four per- and four inter-radial. Soon the process of constriction is completed, the saucer-like bodies separate from one another, and each, turning upside down, begins to swim about as a small jelly-fish called an *ephyra* (*D*, *E*). The umbrella of the ephyra is divided into eight long bifid arms (*a*) with deep (per-radial or inter-radial) notches : it has of course carried away with it a segment of the stomach with the gastric ridges of the scyphistoma : during the process of constriction this becomes closed in on the proximal or ex-umbrellar side, while on the sub-umbrellar side it remains open, and its edges grow out to form a manubrium. On each gastric ridge appears a single gastric filament, soon to be followed by others, and in the notches at the extremities of the eight arms tentaculocysts are now recognizable. In the meantime the spacious enteric cavity is continued into the eight arms in the form of wide radiating canals.

As the ephyra grows, the ad-radial regions—at first deeply notched—grow more rapidly than the rest, the result being that the notches become gradually filled up, and the umbrella, from an eight-rayed star, becomes a nearly circular disc. Four oral arms are developed and numerous marginal tentacles, and the ephyra gradually assumes the form of the adult Aurelia.

Thus the life-history of Aurelia differs in several marked respects from that of any of the Hydrozoa. There is, in a sense, an alternation of generations as in Obelia, the sexual generation being represented by the adult Aurelia, the asexual generation by the scyphistoma. But instead of the medusa being developed either as a bud on a branched colony, as in Hydroidea, or by direct metamorphosis of a polype, as in Trachylinæ, it is formed by the metamorphosis of an ephyra developed as one of several transverse segments of a polype ; so that the life-history might be described as a metamorphosis complicated by multiplication in the larval (scyphistoma) condition, rather than a true alternation of generations.

It has been shown that, under exceptional circumstances, the egg of Aurelia develops into scyphistomæ which do not undergo transverse division, the entire scyphistoma becoming metamorphosed into a single adult.

2. Distinctive Characters and Classification.

The Scyphozoa may be defined as medusoid Cœlenterata, having the same general structure and arrangement of the layers as the medusoid Hydrozoa, but differing from them in the possession of endodermal gastric tentacles; in having gonads the sexual cells of which are lodged in the endoderm and which discharge their products into the digestive cavity; in the absence of a true velum, and, in nearly all cases, in the presence of sense-organs in the form of hollow sense-clubs or tentaculocysts. As in the Hydrozoa, the medusa develops directly from the egg in some Scyphozoa, while in others there is a sort of alternation of generations, a polype-form giving rise to the medusa-form by a process of transverse fission (strobilation). In the majority, however, nothing is known of the life-history, the process of development having been worked out only in a few cases.

The Scyphozoa are divisible into five orders, as follows:—

Order 1.—Lucernaridæ (Stauromedusæ).

Scyphozoa having a conical or vase-shaped umbrella, mostly attached to external objects by an ex-umbrellar peduncle: no tentaculocysts.

Example: *Lucernaria* (Fig. 135).

Order 2.—Coronata.

Scyphozoa having the umbrella divided by a horizontal *coronary groove*: four to sixteen tentaculocysts.

Examples: *Pericolpa* (Fig. 136); *Nausithoë* (Fig. 137).

Order 3.—Cubomedusæ.

Scyphozoa with a four-sided cup-shaped umbrella: four per-radial tentaculocysts.

Example: *Charybdæa* (Fig. 138).

Order 4.—Semæostomeæ (Discomedusæ).

Scyphozoa with a flattened saucer- or disc-shaped umbrella: not fewer than eight tentaculocysts—four per- and four inter-radial; the square mouth produced into four long oral arms.

Example: *Aurelia* (Fig. 130).

Order 5.—Rhizostomeæ.

Scyphozoa having the mouth obliterated by the growth across it of the oral arms: the stomach is continued into canals which open by funnel-shaped apertures on the edges of the arms.

Example: *Pilema* (Fig. 139).

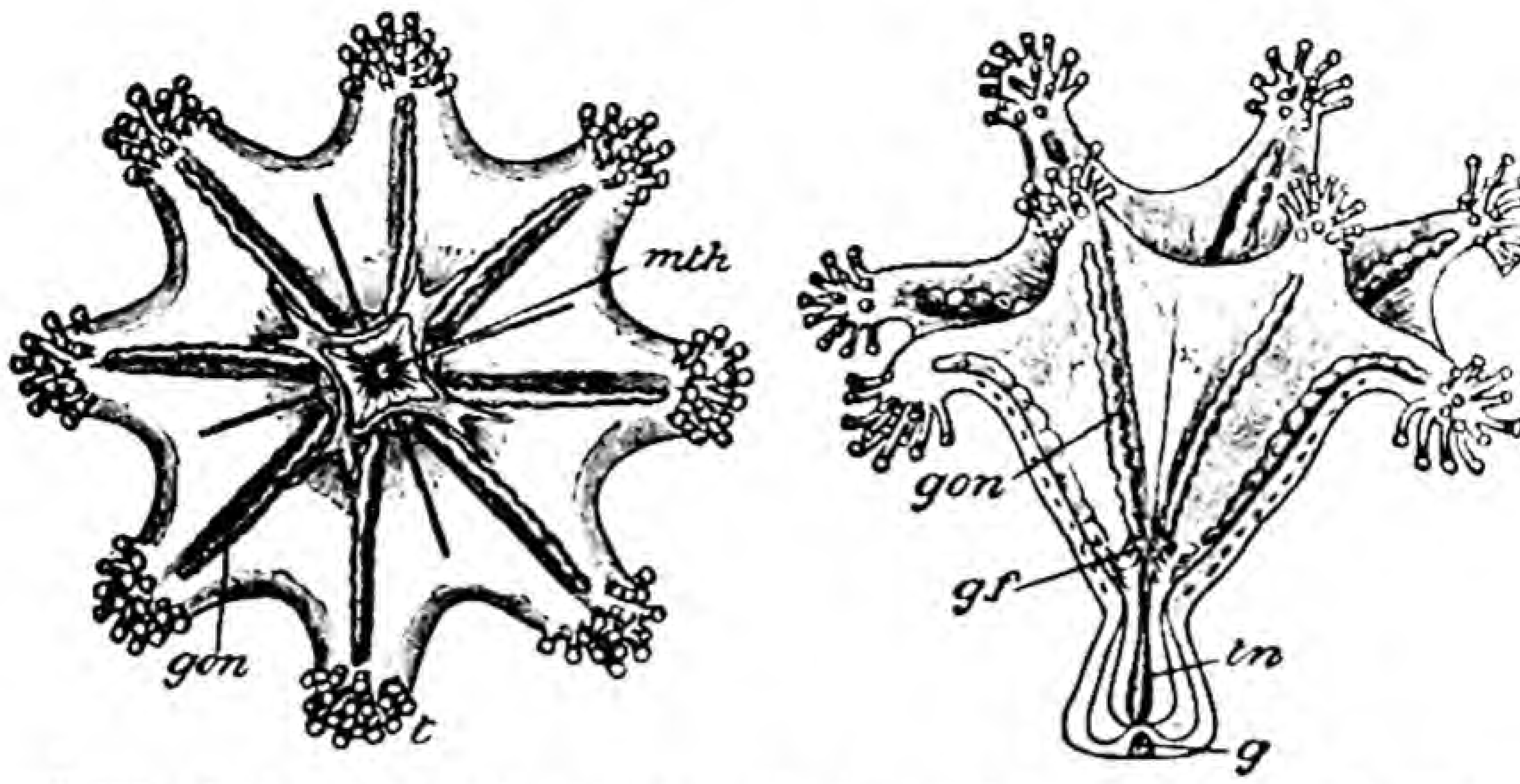


FIG. 135.—**Lucernaria.** *A*, oral aspect; *B*, from the side. *g.* foot-gland; *g. f.* gastric filaments; *gon.* gonad; *mth.* mouth; *t.* tentacles; *tn.* tænioles. (After Claus.)

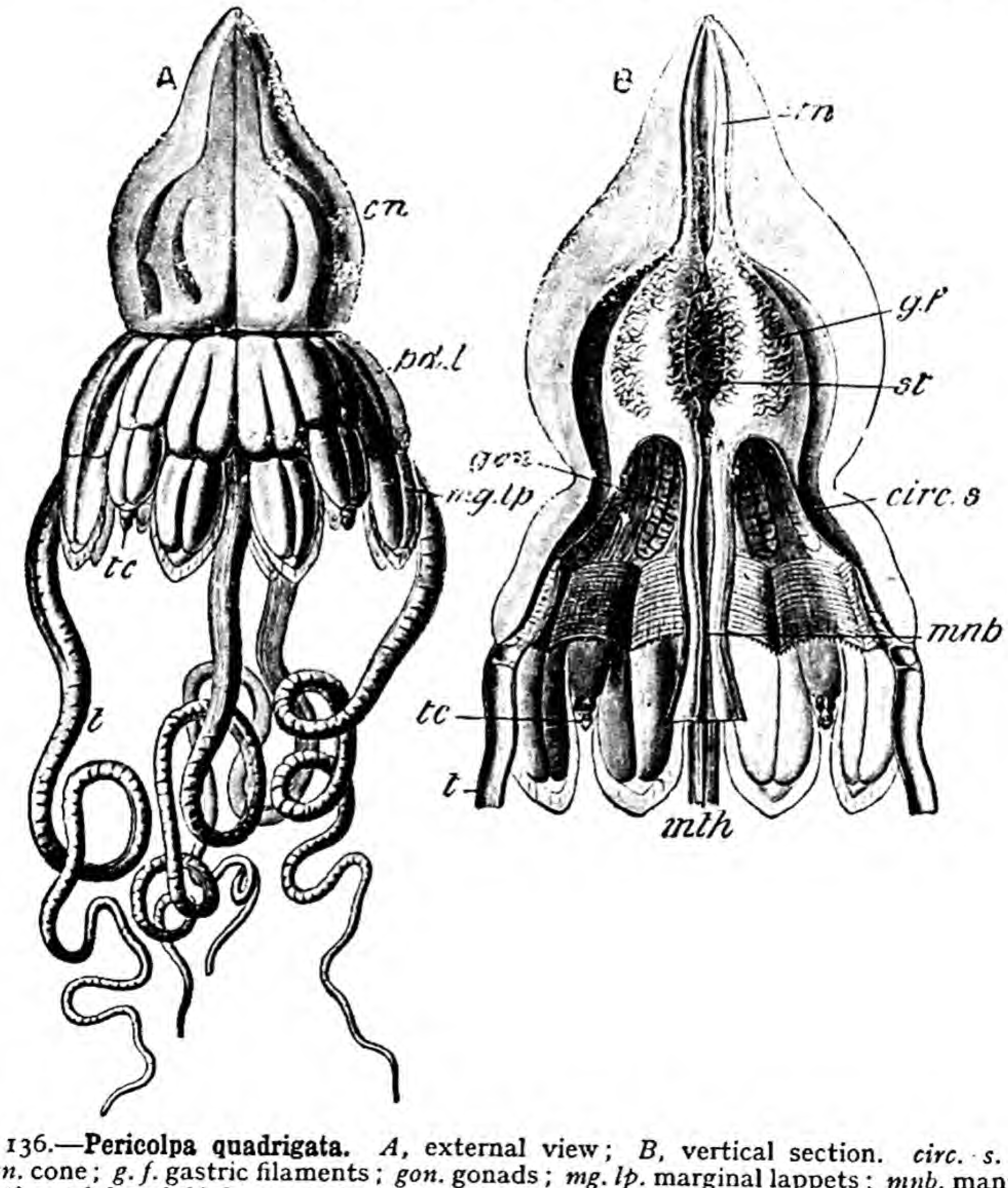


FIG. 136.—**Pericolpa quadrigata.** *A*, external view; *B*, vertical section. *circ. s.* circular sinus; *cn.* cone; *g. f.* gastric filaments; *gon.* gonads; *mg. lp.* marginal lappets; *mnb.* manubrium; *mth.* mouth; *pd. l.* pedal lobes; *st.* stomach; *t.* tentacles; *tc.* tentaculocysts; *tn.* tænioles. (After Haeckel.)

ORDER 1.—LUCERNARIDÆ (STAUROMEDUSÆ).

Lucernaria (Fig. 135), a genus not uncommon on the British coasts, is in one respect even more like a scyphistoma, since it is attached by a peduncle developed from the centre of the ex-umbrella. The margin of the umbrella is prolonged into eight short hollow ad-radial arms, bearing at their ends groups of short adhesive tentacles (*t.*). As in the scyphistoma, each gastric ridge contains an infundibulum, lined with ectoderm and opening on the sub-umbrella. The gastric filaments (*g. f.*) are very numerous and the gonads (*gon.*) are band-like. There are no sense-organs in Lucernaria. In an allied genus, *Halicystus*, there are eight per-radial and inter-radial marginal bodies (*anchors*) of the nature of reduced and modified tentacles, each surrounded at its base by a cushion-like thickening containing many adhesive cells. Internal to each anchor on the sub-umbrellar side is a pigment spot. *Stenocyphus* is an allied form which probably is able to move by creeping (looping) movements like those of a leech. *Capria* has no tentacles. The *Depastridæ* have an almost entire margin fringed with tentacles.

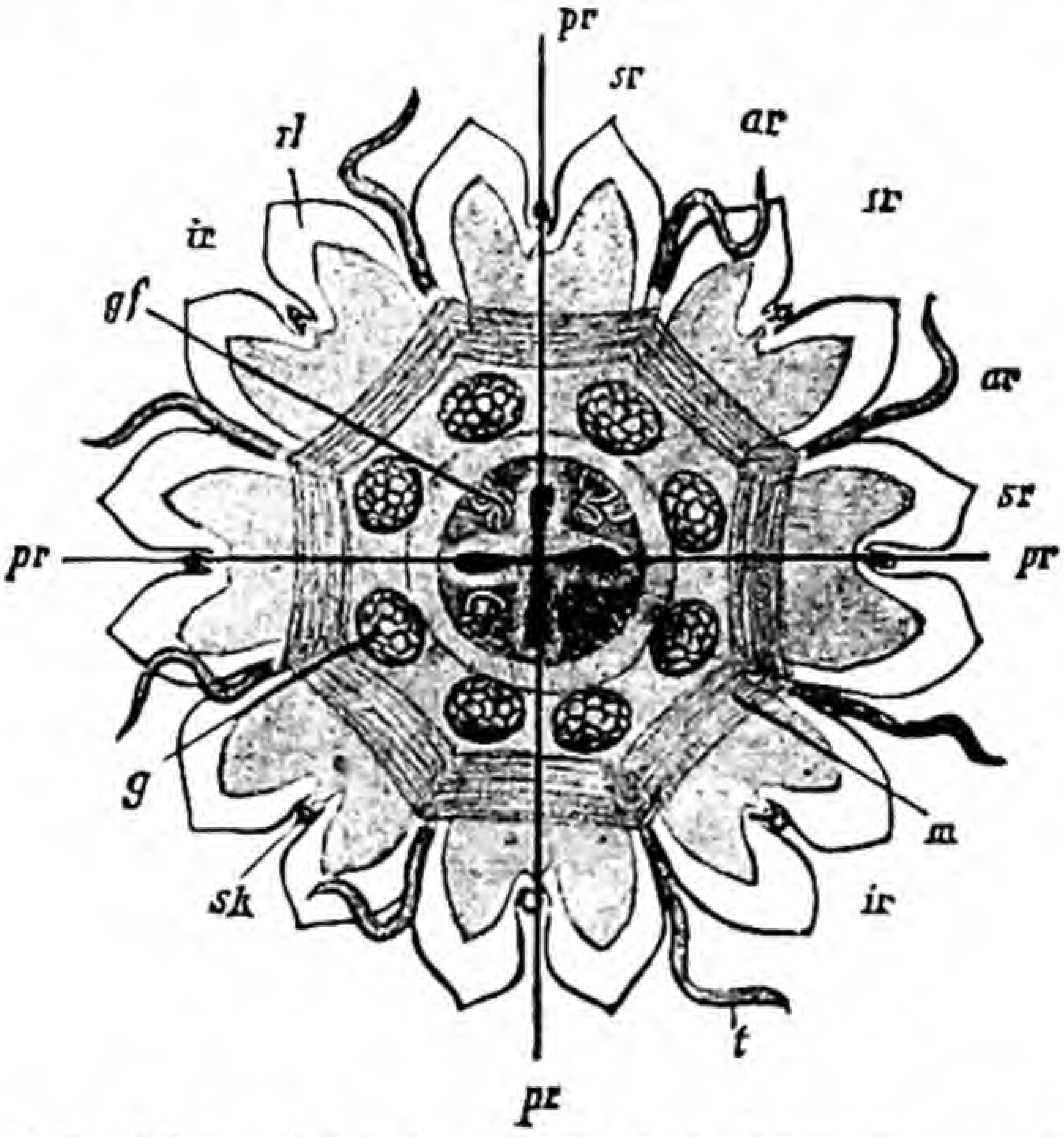


FIG. 137.—**Nausithoë.** The entire animal from the oral aspect. *ar.* adradii; *g.* gonads; *g. f.* gastric filaments; *ir.* inter-radii; *m.* circular muscle of subumbrella; *pr.* per-radii; *rl.* tentaculocysts; *sr.* subradii; *t.* tentacles. The black cross in the centre represents the mouth. (From Lang's *Comparative Anatomy*.)

ORDER 2.—CORONATA.

This group includes a number of rare and beautiful Medusæ of curiously complex structure, of which *Pericolpa* may be taken as an example. The umbrella (Fig. 136) is usually conical, and is divided by a horizontal furrow (*coronary groove*) into an apical region or *cone* (*cn.*) and a marginal region or *crown*; the crown is again divided by a second, rather irregular horizontal furrow into a series of *pedal lobes* (*pd. l.*), adjacent to the cone, and a series of *marginal lappets* (*mg. lp.*), forming the free edge of the bell. In some of the Coronata, such as *Pericolpa*, the pedal lobes and marginal lappets correspond (*i.e.*, are in the same radii); in others (*Periphylla, Ephyropsis*) they alternate.

In *Pericolpa* four of the pedal lobes, inter-radial in position, bear tentaculocysts (*tc.*); four others, per-radially situated, give origin to long, hollow tentacles (*t.*). In the more complex genera there are eight additional ad-radial tentacles.

The mouth (*mth.*) is very large, and leads by a wide manubrium (*mnb.*) into a spacious stomach (*st.*), which is continued quite to the apex of the cone. In the wall of the stomach are four wide per-radial slits, leading into an immense circular sinus (*circ. s.*). As in Lucernaria, there are four wide inter-radial infundibula. The gastric filaments (*g. f.*)

are very numerous, and the elongated U-shaped gonads (*gon.*) are eight in number and ad-radial.

The coronary groove is characteristic of the group: but in other points—such as the number of pedal and marginal lobes, tentaculocysts, and tentacles—there is great variation. *Pericolpa* and its allies (*Peromedusæ*) resemble the *Lucernarida* and the members of the order *Cubomedusæ* in the presence of tænioles and inter-radial septa: *Ephyropsis* and its allies (*Canostomæ*) resemble the order *Discomedusæ* in the absence of these structures. The scyphistoma stage of *Nausithoë* (Fig. 137) lives as a parasite in the interior of a horny sponge.

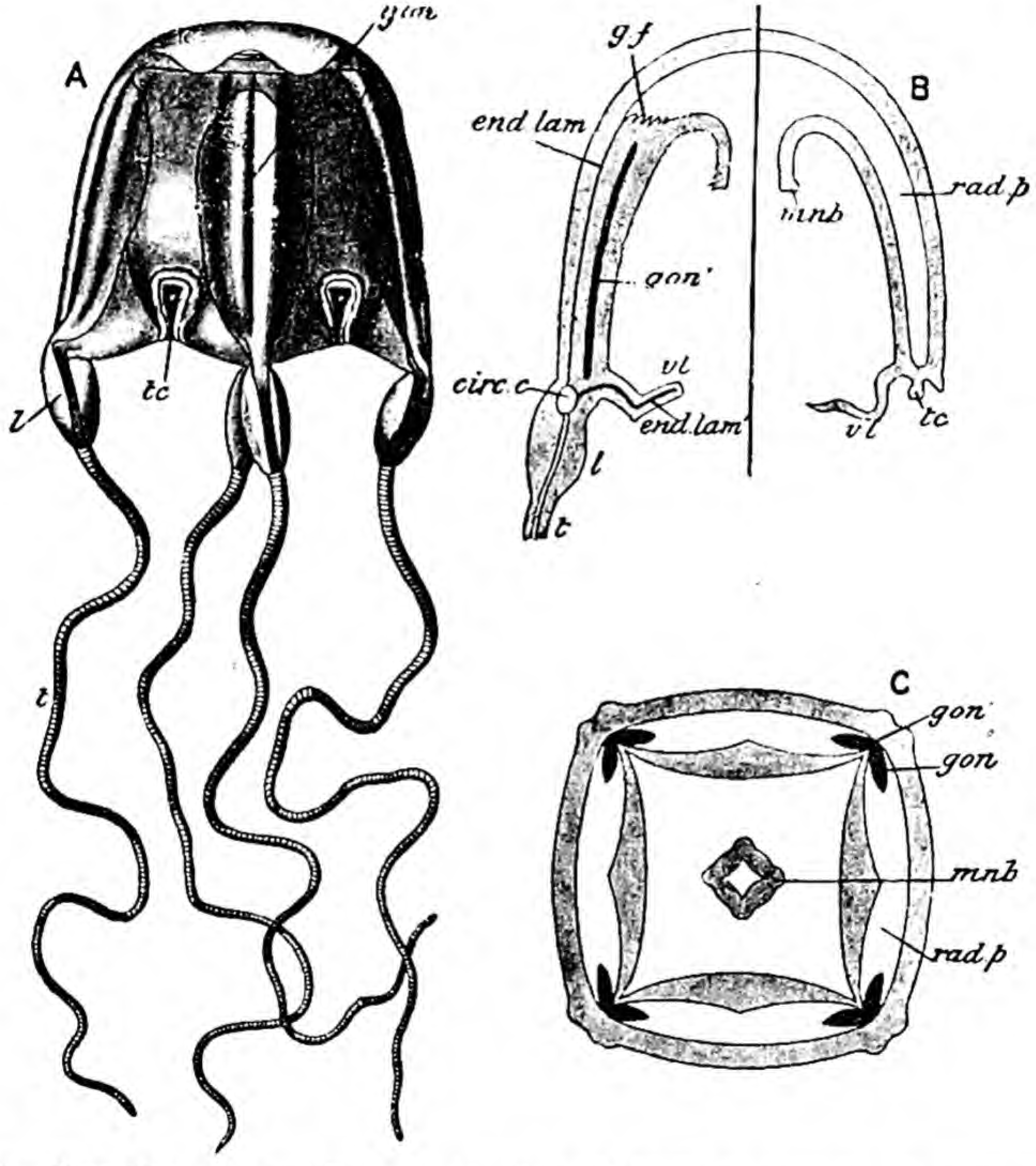


FIG. 138.—**Charybdæa marsupialis.** *A*, side view of the entire animal; *B*, vertical section passing on the left side through an inter-radius, on the right through a per-radius; *C*, transverse section. *circ. c.* circular canal; *end. lam.* endoderm lamella; *end. lam'.* its prolongation into the velarium; *g. f.* gastric filaments; *gon.* gonad; *gon'.* septum separating gonads; *l.* lappet; *mnb.* manubrium; *rad. p.* radial pouch; *t.* tentacle; *tc.* tentaculocyst; *vl.* velarium. (After Claus, somewhat altered.)

ORDER 3.—CUBOMEDUSÆ.

The Jelly-fishes forming this order are, as the name implies, of a more or less cubical form, resembling a deep bell with somewhat flattened top and square transverse section. They resemble the hydrozoan Medusæ more than any of the other Scyphozoa. The best known species, *Charybdæa marsupialis* (Fig. 138), is about 5 cm. in diameter and of very firm consistency.

As in the lower Coronata, the margin of the umbrella bears four tentacles (*t.*) and four tentaculocysts (*tc.*), but the position of these organs is reversed, the tentaculocysts being per-radial, the tentacles inter-radial. The tentaculocysts are set in deep marginal notches, and the tentacles spring from conspicuous gelatinous lobes (*l.*), which probably answer to the pedal lobes of the preceding order. These pedal lobes sometimes bear a number of supplementary tentacles.

The margin of the umbrella is produced, in most cases but not in all, into a horizontal shelf (*vl.*), resembling the velum of the hydroid Medusæ, but differing from it in containing a series of branched vessels (*end. lam'.*) continuous with the canal-system and of course lined with endoderm. In the Hydrozoa, it will be remembered, the velum is formed simply of a double layer of ectoderm with a supporting layer of mesoglœa. Such a false velum, like the produced thin edge of the umbrella in Aurelia, is known as a *velarium*.

The mouth is situated at the end of a short manubrium (*mnb.*) leading into a wide stomach, from which go off four very broad shallow per-radial pouches (*rad. p.*), occupying the whole of the four flat sides of the umbrella, and separated from one another by narrow inter-radial septa or partitions (*mesenteries*) placed at the four corners. These pouches are equivalent to wide radial canals, and the partitions between them to a poorly developed endoderm lamella (*end. lam.*). At the margin of the umbrella the pouches communicate with one another by apertures in the septa, so that a kind of circular canal is produced (*circ. c.*), which is divided into chambers by the mesenteries. Near the junction of the gastric pouches with the stomach are the usual four groups of gastric filaments (*g. f.*).

The gonads (*gon.*) are four pairs of narrow plate-like organs, attached one along each side of each inter-radial septum. The nervous system takes the form of a sinuous nerve-ring round the margin of the bell, bearing a distinct group of nerve-cells at the base of each tentaculocyst and tentacle. The Cubomedusæ are the only Scyphozoa which, like the Hydrozoa, have a complete nerve-ring. The tentaculocysts are very complex, each bearing a lithocyst and several eye-spots. Along with these eye-spots some Cubomedusæ have more highly developed eyes possessing a lense, a retina, and pigment.

ORDER 4.—SEMÆOSTOMEÆ (DISCOMEDUSÆ).

Aurelia aurita belongs to this order, and has already been dealt with in great detail as an example of the whole class. Along with it the present order contains a vast number of Scyphozoa, which are commonly known as the "Disc-jellies" or "Sea-blubbers."

The umbrella is always comparatively flat, having the form of an inverted saucer. The edge is produced primarily into eight pairs of marginal lappets, but in some of the more highly differentiated forms the number both of lappets and of tentaculocysts becomes greatly increased. Most of the Semæostomeæ are large, and one—*Cyanea arctica*—may attain a diameter of 2 metres and upwards, while its marginal tentacles reach the astonishing length of 40 metres or about 130 feet. But in spite of their size and apparent solidity, the amount of solid matter in these great Jelly-fishes is extraordinarily small; some of them have been proved to contain more than 99 per cent. of sea-water.

The marginal tentacles are hollow and often of great length (Fig. 130). There are four oral arms (Fig. 130, *or. a.*), each resembling a leaf folded along its midrib, and having more or less frilled edges.

The arrangement of the enteric cavity and its offshoots presents an interesting series of modifications. In no case are there any tænioles or inter-radial septa (mesenteries). The stomach-lobes give off well-defined radial canals, which are frequently more or less branched, often unite into complex networks, and sometimes open into a circular canal round the margin of the umbrella. The order is subdivided into three families: the *Pelagidæ* with *Pelagia noctiluca*, a form famous for its phosphorescence, the *Cyaneidæ* with the giant *Cyanea arctica*, and the *Ulmaridæ* with *Aurelia aurita*.

ORDER 5.—RHIZOSTOMEÆ.

In the Rhizostomeæ marginal tentacles are absent. In the course of development each of the original four oral arms (Fig. 139, *or. a.*) becomes divided longitudinally, the adult members of the group being characterized by the presence of eight arms which are often of great length and variously lobed and folded so as to present a more or less root-like appearance.

As in the Semæostomeæ a network of canals is found in the umbrella, but an extraordinary change has befallen the oral or ingestive portion of the enteric system. Looking

at the oral or lower surface of one of these Jelly-fishes, such as *Pilema*, no mouth is to be seen, but a careful examination of the oral arms shows the presence of large numbers—hundreds, or even thousands in some cases—of small funnel-like apertures (Fig. 139, *B*, *C*, *s. mth.*) with frilled margins. Rhizostomes have been found with prey of considerable size, such as fishes, embraced by the arms and partly drawn into these apertures, which are therefore called the *suctorial mouths*. They lead into canals in the thickness of the arms (*B*, *c.*), the lesser canals unite into larger, and then finally open into the stomach (*st.*). We thus get a *polystomatous* or many-mouthed condition which is practically unique in the animal kingdom, the only parallel to it being furnished by the Sponges, in which the inhalant pores are roughly comparable with the suctorial mouths of a Rhizostome.

It has been found that this characteristic arrangement is brought about by certain changes taking place during growth. The young Rhizostome has a single mouth in the

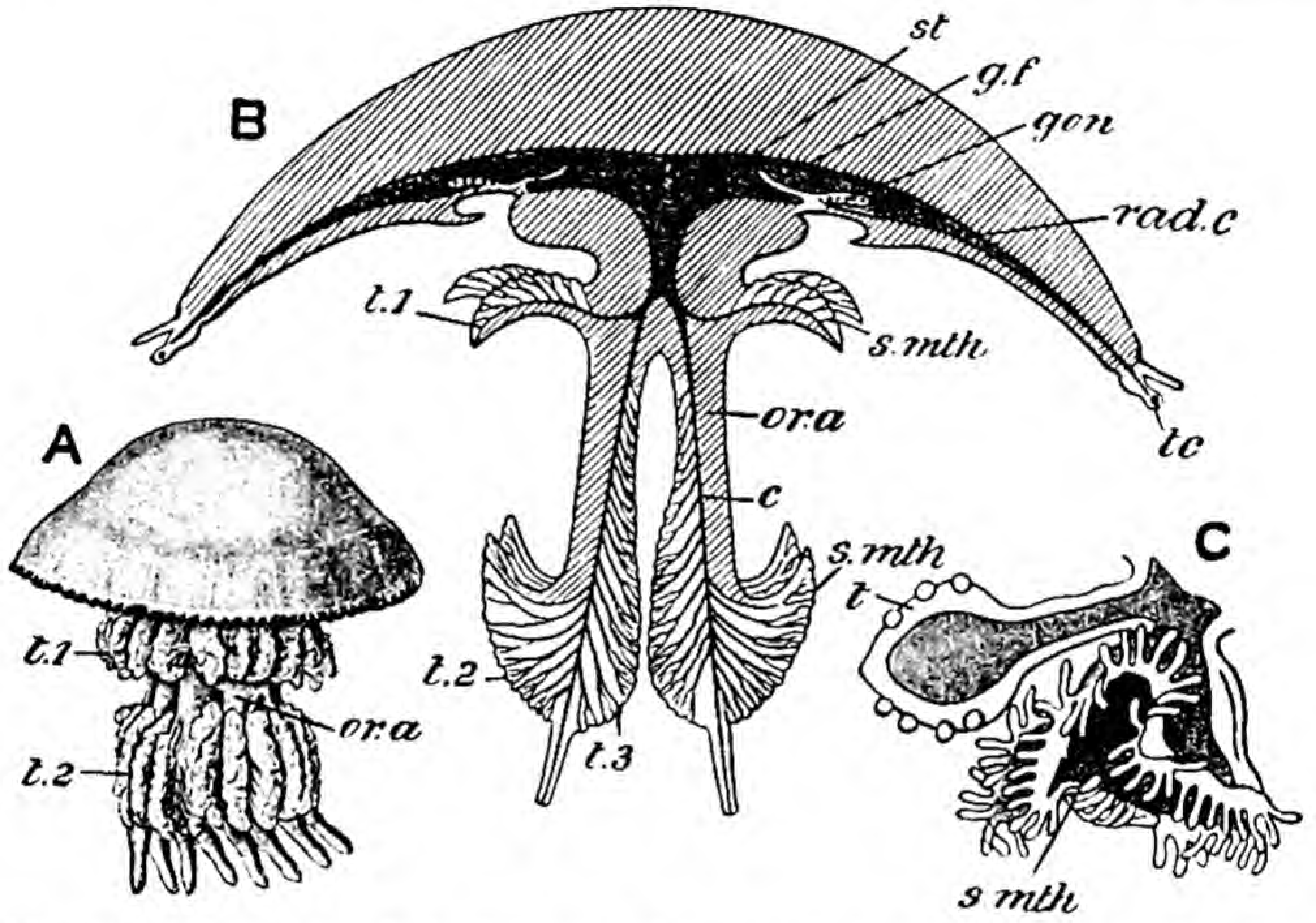


FIG. 139.—**Pilema pulmo.** *A*, side view of the entire animal; *B*, vertical section, diagrammatic; *C*, one of the suctorial mouths, magnified. *c.* arm canal; *g. f.* gastric filaments; *gon.* gonads; *or. a.* oral arms; *rad. c.* radial canal; *s. mth.* suctorial mouths; *st.* stomach; *t1*, *t2*, *t3*, tentacles on oral arms. (After Cuvier, Claus, and Huxley.)

usual position, and more or less leaf-like arms, folded along the midrib so as to enclose a deep groove, from which secondary grooves pass, like the veins of a leaf, towards the edge of the arm. As development proceeds, these grooves become converted into canals by the union of their edges, thus forming a system of branching tubes opening proximally into the angles of the mouth and distally by small apertures—the suctorial mouths—on the edges of the arms. At the same time the proximal ends of the arms grow towards one another and finally unite across the mouth, closing it completely, and forming a strong horizontal *brachial disc*, which in the adult occupies the centre of the sub-umbrellar surface.

The gastric filaments are usually very numerous. In the higher Rhizostomeæ a remarkable modification is produced in connection with the sub-genital pouches; the four pouches approach the centre and fuse with one another, forming a single spacious chamber, the *sub-genital portico*, which lies immediately below the floor of the stomach and above the brachial disc.

Additional Remarks on the Scyphozoa.

The Scyphozoa are all marine, and the majority are pelagic, *i.e.*, swim freely on the surface of the ocean. A few inhabit the deep sea, and have been dredged from as great a depth as 2000 fathoms. Nearly all are free-swimming in the adult state: some, however, live on coral-reefs or mud-banks, and are found resting, in an inverted position, on the ex-umbrella; and a few, such as Lucernaria, are able to attach themselves by a definite ex-umbrellar peduncle.

Many of the Scyphozoa are semi-transparent and glassy, but often with brilliantly coloured gonads, tentacles, or radial canals. In many cases the umbrella, oral arms, etc., are highly coloured, and some species, *e.g.*, Pelagia noctiluca, are phosphorescent. They are all carnivorous, and although mostly living upon small organisms, are able, in the case of the larger species, to capture and digest Crustaceans and Fishes of considerable size. In many cases small fishes accompany the larger forms and take shelter under the umbrella.

Considering the extremely perishable nature of these organisms, and the fact that many of them contain not more than 1 per cent. of solid organic matter, it is not to be expected that many of them should have left traces of their existence in the fossil state. Nevertheless, fossil Scyphozoa have been described from Cambrian and Ordovician rocks; and, in the finely grained limestone of Solnhofen, in Bavaria, belonging to the Upper Jurassic period, remarkably perfect impressions of Jelly-fishes have been found, some of them readily recognizable as Discomedusæ.

CLASS III.—ACTINOZOA.

1. Example of the Class—A Sea-anemone.

Urticina (Tealia) crassicornis.

Sea-anemones are amongst the most abundant and best known of shore-animals. They are found attached to rocks, sea-weeds, shells, etc., either in rock-pools or on rocks left high and dry by the ebbing tide. Usually their flower-like form and brilliant colour make them very conspicuous objects, but many kinds cover themselves more or less completely with sand and stones, and contract so much when left uncovered by water that they appear like soft, shapeless lumps stuck over with stones, and thus easily escape observation. Any of the numerous species will serve as an example of the group: the form specially selected is the "Dahlia Wartlet" (*Urticina* (*Tealia*) *crassicornis*), one of the commonest British species.

External Characters.—*Urticina* (Fig. 140, *A*) has the form of a cylinder, the diameter of which slightly exceeds its height. It is often as much as

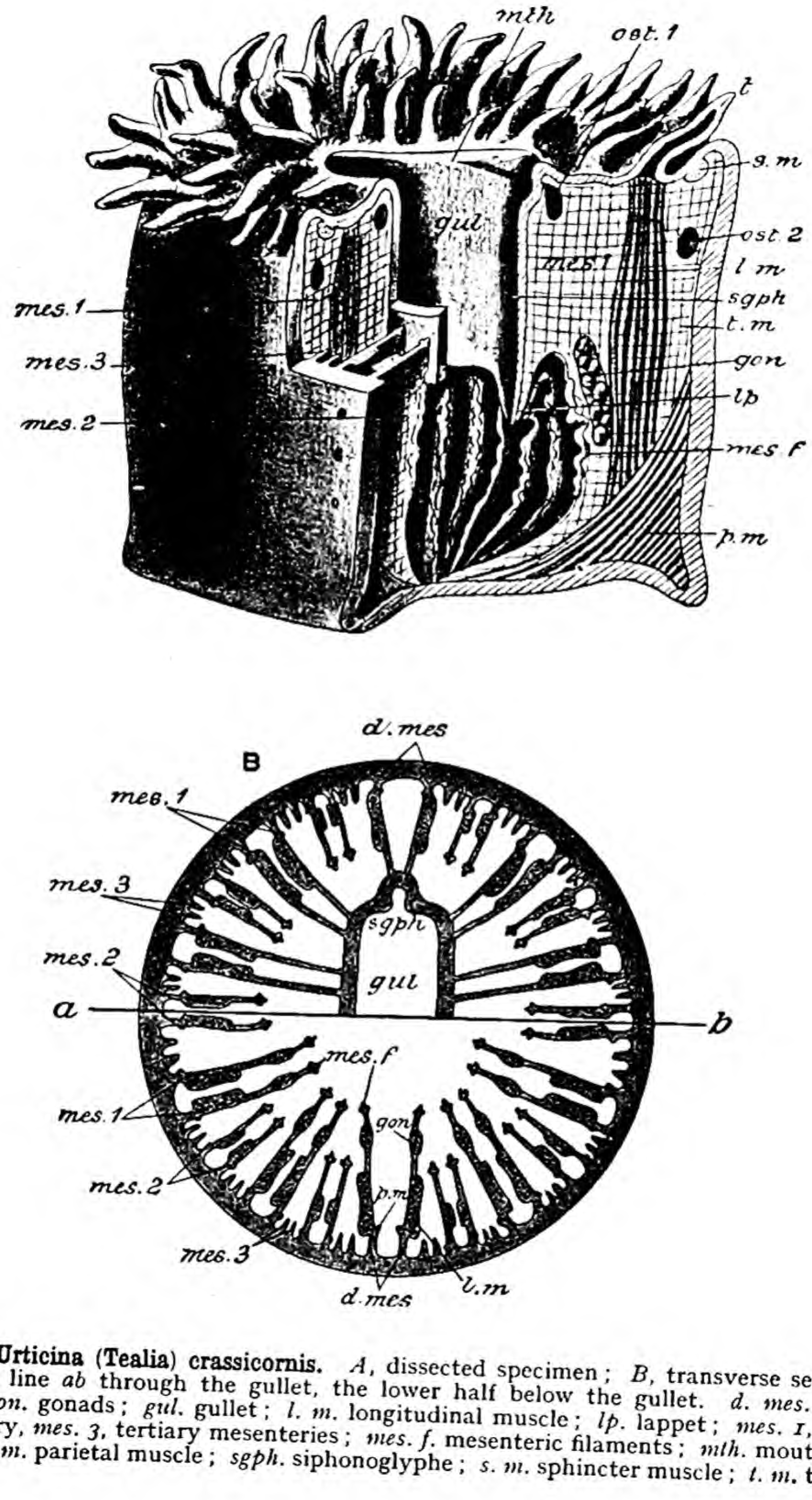


FIG. 140.—**Urticina (Tealia) crassicornis.** *A*, dissected specimen; *B*, transverse section, the half above the line *ab* through the gullet, the lower half below the gullet. *d. mes.* directive mesenteries; *gon.* gonads; *gul.* gullet; *l. m.* longitudinal muscle; *lp.* lappet; *mes. 1*, primary, *mes. 2*, secondary, *mes. 3*, tertiary mesenteries; *mes. f.* mesenteric filaments; *mth.* mouth; *ost. 1*, *ost. 2*, ostia; *p. m.* parietal muscle; *sgph.* siphonoglyphe; *s. m.* sphincter muscle; *t. m.* transverse muscle.

3 inches (8 cm.) across, is of a green or red colour, and habitually covers itself with bits of shell, small stones, etc. It is attached to a rock or other support by a broad sole-like *base*, sharply separated from an upright cylindrical wall or *column*, the surface of which is beset with rows of adhesive warts or tubercles : at its upper or distal end the column passes into a horizontal plate, the *disc* or *peristome*. In the middle of the disc, and slightly elevated above its surface, is an elongated slit-like aperture, the *mouth* (*mth.*), from which streaks of colour radiate outwards. Springing from the disc and encircling the mouth are numerous short conical *tentacles* (*t.*), which appear at first sight to be arranged irregularly, but are actually disposed in five circlets, of which the innermost contains five, the next five, the third ten, the fourth twenty, and the fifth or outermost forty, making a total of eighty.

Obviously the Sea-anemone is a *polype*, formed on the same general lines as a hydroid polype or a scyphistoma, but differing from them in having numerous tentacles arranged in multiples of five, and in the absence of an oral cone, the mouth being nearly flush with the surface of the disc. Its great size and bulk, and the comparative firmness of its substance, are also striking points of difference between Urticina and the polypes belonging to the classes Hydrozoa and Scyphozoa.

Enteric System.—Still more fundamental differences are found when we come to consider the internal structure. The mouth does not lead at once into a spacious undivided enteric cavity, but into a short tube (*gul.*), having the form of a flattened cylinder, which hangs downwards into the interior of the body, and terminates in a free edge, produced at each end of the long diameter into a descending lobe or *lappet* (*lp.*). This tube is the *gullet* or *stomodæum.* Its inner surface is marked with two longitudinal grooves (*A* and *B*, *sgph.*), placed one at each end of the long diameter, and therefore corresponding with the lappets : they are known as the gullet-grooves or *siphonoglyphes.*

The gullet does not simply hang freely in the enteric cavity, but it is connected with the body-wall by a number of radiating partitions, the complete or *primary mesenteries* (*mes. 1*) : between these are incomplete *secondary mesenteries* (*mes. 2*), which extend only part of the way from the body-wall to the gullet, and *tertiary mesenteries* (*mes. 3*), which are hardly more than ridges on the inner surface of the body-wall. Thus the entire internal cavity of a Sea-anemone is divisible into three regions : (1) the *gullet* or *stomodæum,* communicating with the exterior by the mouth, and opening below into (2) a single main digestive cavity, the *stomach* or *cœlenteron,* which gives off (3) a number of radially arranged cavities, the *inter-mesenteric chambers.* It is obvious that we may compare the gullet and stomach with the similarly named structures in the scyphistoma-stage of Aurelia, and the mesenteries with the gastric ridges. A further correspondence is furnished by the presence of an aperture or *ostium* (*ost. 1*) in each mesentery, placing the adjacent inter-

mesenteric chambers in direct communication with one another: in Urticina a second ostium (*ost. 2*) is present near the outer edge of the mesentery. Moreover, the free edge of the mesentery below the gullet is produced into a curious twisted cord, the *mesenteric filament* (*mes. f.*), answering to a gastric filament of the Scyphozoa. In many Sea-anemones the mesenteric filaments are produced into slender threads—the *acontia*—which may be protruded through the mouth or through special apertures (*cinclides*) of the body-wall (Fig. 141, *A*).

The general arrangement of the **cell-layers** is the same as in the two preceding classes. The body-wall (Fig. 141)—base, column, and disc—consists of a layer of ectoderm outside, one of endoderm within, and between them an

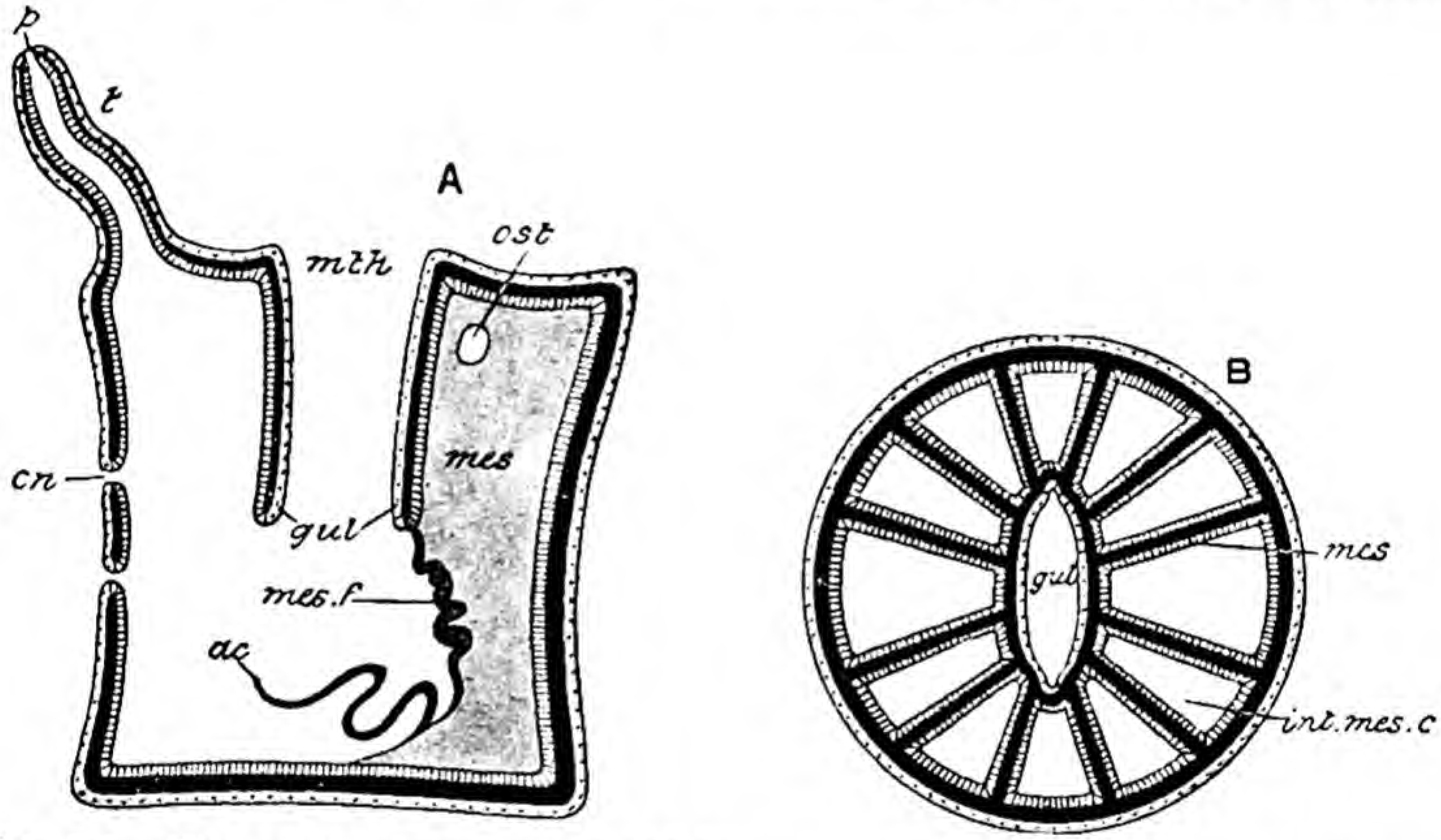


FIG. 141.—Diagrammatic vertical (*A*) and transverse (*B*) sections of a **Sea-anemone.** The ectoderm is dotted, the endoderm striated, the mesoglœa black. *ac.* acontium; *cn.* cinclis; *gul.* gullet; *int.mes.c.* inter-mesenteric chamber; *mes.* mesentery; *mes. f.* mesenteric filament; *mth.* mouth; *ost.* ostium; *p.* pore; *t.* tentacle.

intermediate layer or mesoglœa, which is extremely thick and tough. The gullet (*gul.*) is lined with ectoderm, and its outer surface—*i.e.*, that facing the inter-mesenteric chambers—is endodermal. The mesenteries (*mes.*) consist of a supporting plate of mesoglœa, covered on both sides by endoderm. The tentacles (*t.*) are hollow out-pushings of the disc, and contain the same layers.

Muscular System.—Sea-anemones perform various characteristic movements: the column may be extended or retracted, the tentacles extended to a considerable length, or drawn back and completely hidden by the upper end of the column being folded over them like the mouth of a bag; the gullet, and even the mesenteries, may be partially everted through the mouth; and lastly, the whole animal is able, very slowly, to change its position by creeping movements of its base.

These movements are performed by means of a very well-developed set of *muscles*. A mesentery examined from the surface is seen to be traversed by definite fibrous bands, the two most obvious of which are the *longitudinal* or *retractor muscle* (Fig. 140, *l. m.*), running as a narrow band from base to disc, and the *parietal muscle* (*p. m.*), passing obliquely across the lower and outer angle of the mesentery. Both these muscles are very thick, and cause a projection or bulging on one side of the mesentery, specially obvious in a transverse section (*B*, *l. m.*) : a third set of fibres, forming the *transverse muscle* (*t. m.*), crosses the longitudinal set at right angles, but is not specially prominent. The longitudinal muscles shorten the mesentery, and draw the disc downwards or towards the base, thus retracting the tentacles; the parietal muscles approximate the column to the base, and the transverse fibres produce a narrowing of the mesentery and thus, opposing the action of the longitudinal muscles, act as extensors of the whole body. The withdrawal of disc and tentacles, during complete retraction, has been compared to the closure of a bag by tightening the string, and is performed in much the same way, the string being represented by a very strong band of fibres, the *circular* or *sphincter muscle* (*s. m.*), which encircles the body at the junction of the column and disc.

The foregoing muscles can all be seen by the naked eye, or under a low magnifying power. They are supplemented by fibres, only to be made out by microscopic examination, occurring both in the body-wall and in the tentacles. The latter organs, for instance, are able to perform independent movements of extension and retraction by means of delicate transverse and longitudinal fibres.

It was mentioned above that the thickness of the longitudinal and parietal muscles produces a bulging on one surface of the mesenteries. A transverse section shows that the arrangement of the mesenteries and of their muscles is very definite and characteristic (Fig. 140, *B*). At each end of the gullet, opposite the siphonoglyphe, are two mesenteries (*d. mes.*), having their longitudinal muscles turned away from one another : they are distinguished as the *directive mesenteries*, and, in the case of Urticina, there are two couples of directive mesenteries, one at each end of the long axis of the gullet. Of the remaining complete or primary mesenteries there are four couples on each side (*mes. 1*), differing from the directive couples in having the longitudinal muscles turned towards one another. The secondary and tertiary mesenteries (*mes. 2*, *mes. 3*) are also arranged in couples, and in all of them the longitudinal muscles of each couple face one another.

Symmetry.—It will be noticed that Urticina, unlike the typical hydrozoan and scyphozoan polypes, presents a distinct *bilateral symmetry*, underlying, as it were, its superficial radial symmetry. It is divisible into equal and similar halves by two planes only, viz., a *vertical* or *sagittal plane* taken through the

long diameter of the gullet, and a *transverse plane* taken through its short diameter.

The general **microscopic structure** of a Sea-anemone is well shown by a section through a tentacle (Fig. 142). Both ectoderm (*ect.*) and endoderm (*end.*) consist mainly of very long columnar, ciliated epithelial cells, and the mesoglœa (*msgl.*) is not only extremely thick, but has the general characters of connective tissue, being traversed by a network of delicate fibres with interspersed cells. The middle layer has, in fact, ceased to be a mere gelatinous

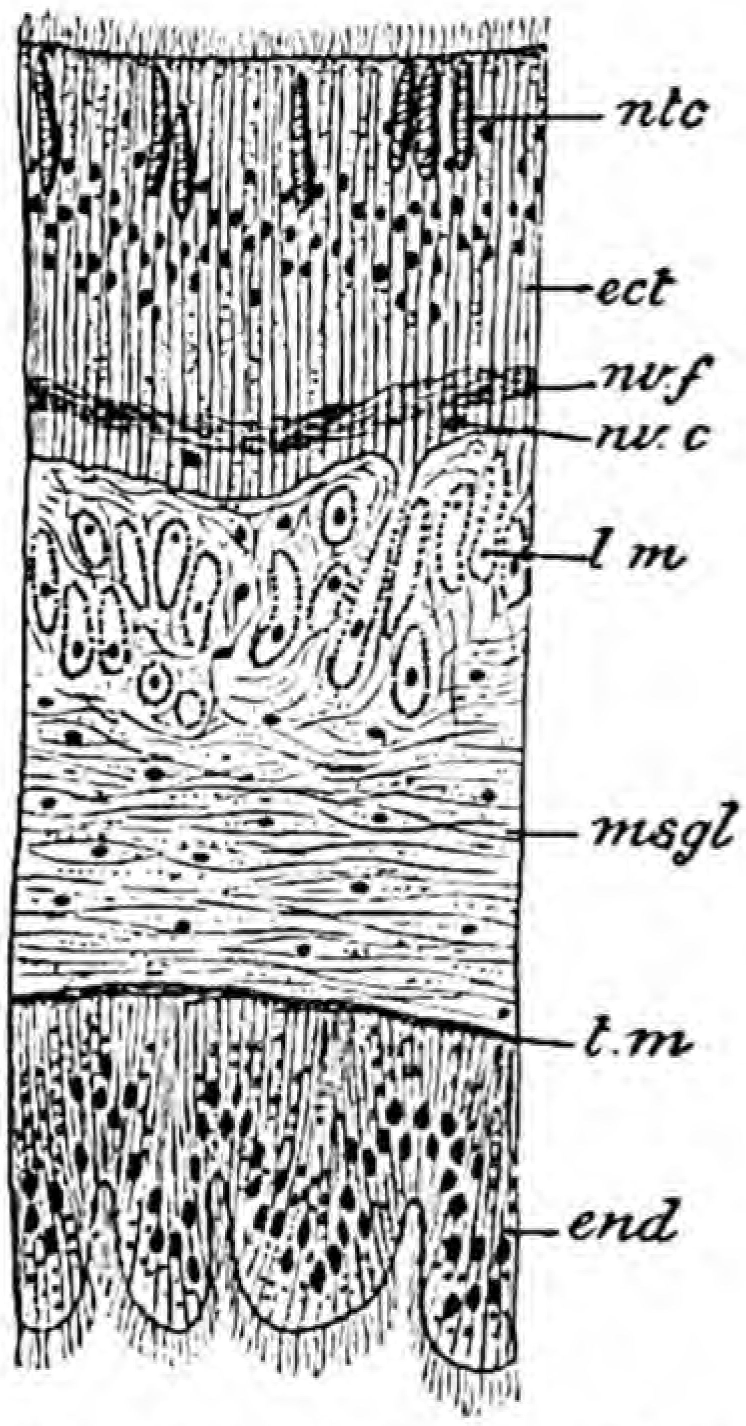


FIG. 142.—**Urticina (Tealia) crassicornis.** Transverse section of tentacle. *ect.* ectoderm; *end.* endoderm; *l. m.* longitudinal muscles; *msgl.* mesoglœa; *nv.c.* nerve-cells; *nv.f.* nerve-fibres; *ntc.* nematocysts; *t.m.* transverse muscles. (After Hertwig.)

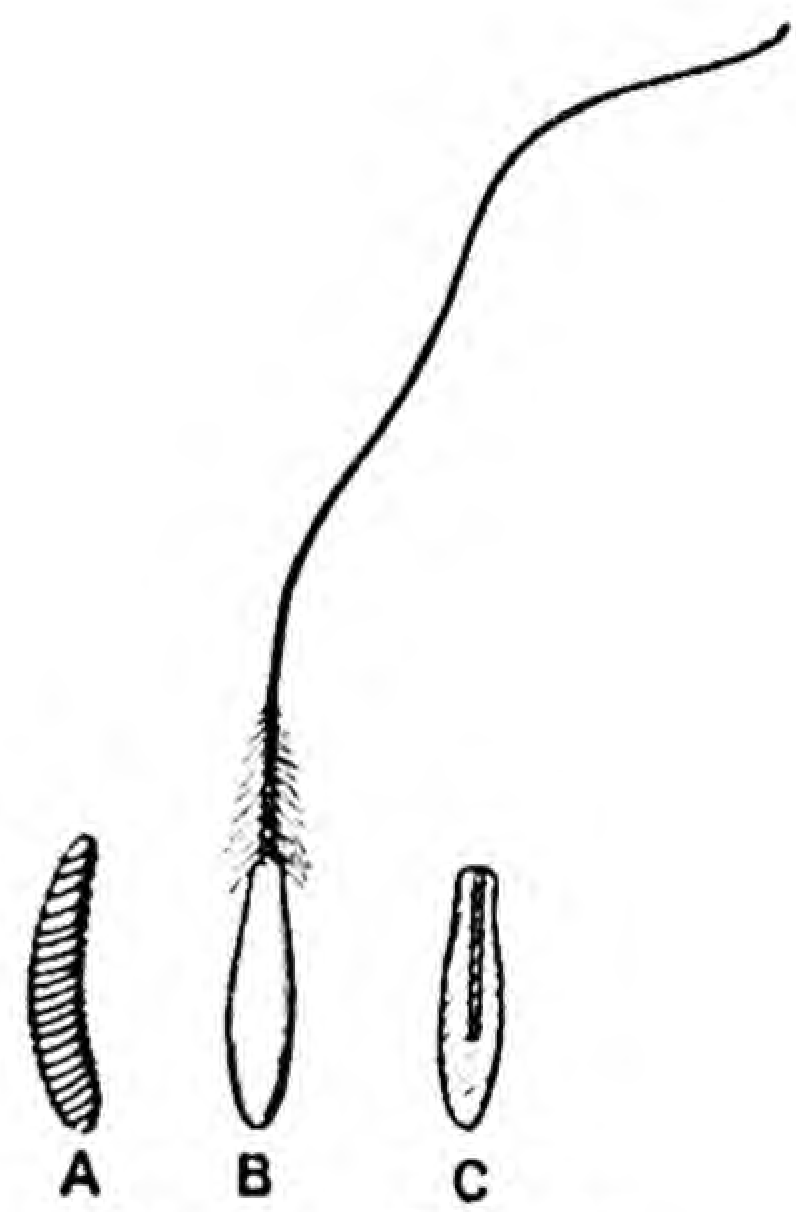


FIG. 143.—Three nematocysts of **Sagartia.** (After Hertwig.)

supporting lamella or *mesoglœa*, and has assumed, to a far greater extent than in any of the lower groups, the characters of an intermediate cell-layer.

Stinging-capsules occur in the ectoderm, and are also very abundant in the mesenteric filaments. They (Fig. 143) resemble in general characters the nematocysts of the Hydrozoa, but are of a more elongated form, and the thread is usually provided at the base with very numerous slender barbs (*B*). Very frequently the coiled thread is readily seen in the undischarged capsule (*A*). Gland-cells (Fig. 144, *gl.*) are very abundant in the ectodermal lining of the gullet and in the mesenteric filaments: the latter are trilobed in section, and

the gland-cells are confined to the middle portion, the lateral divisions being invested with ordinary ciliated cells (*c.*). In virtue of possessing both stinging-capsules and gland-cells, the mesenteric filaments perform a double function. The animal is very voracious, and is able to capture and swallow small Fishes, Molluscs, Sea-urchins, etc. The prey is partly paralysed, before ingestion, by the nematocysts of the tentacles, but the process is completed, after swallowing, by those of the mesenteric filaments. Then as the captured animal lies in the stomach, the edges of the filaments come into close contact with one another and practically surround it, pouring out, at the same time, a digestive juice secreted by their gland-cells.

The muscles described above consist partly of spindle-shaped nucleated

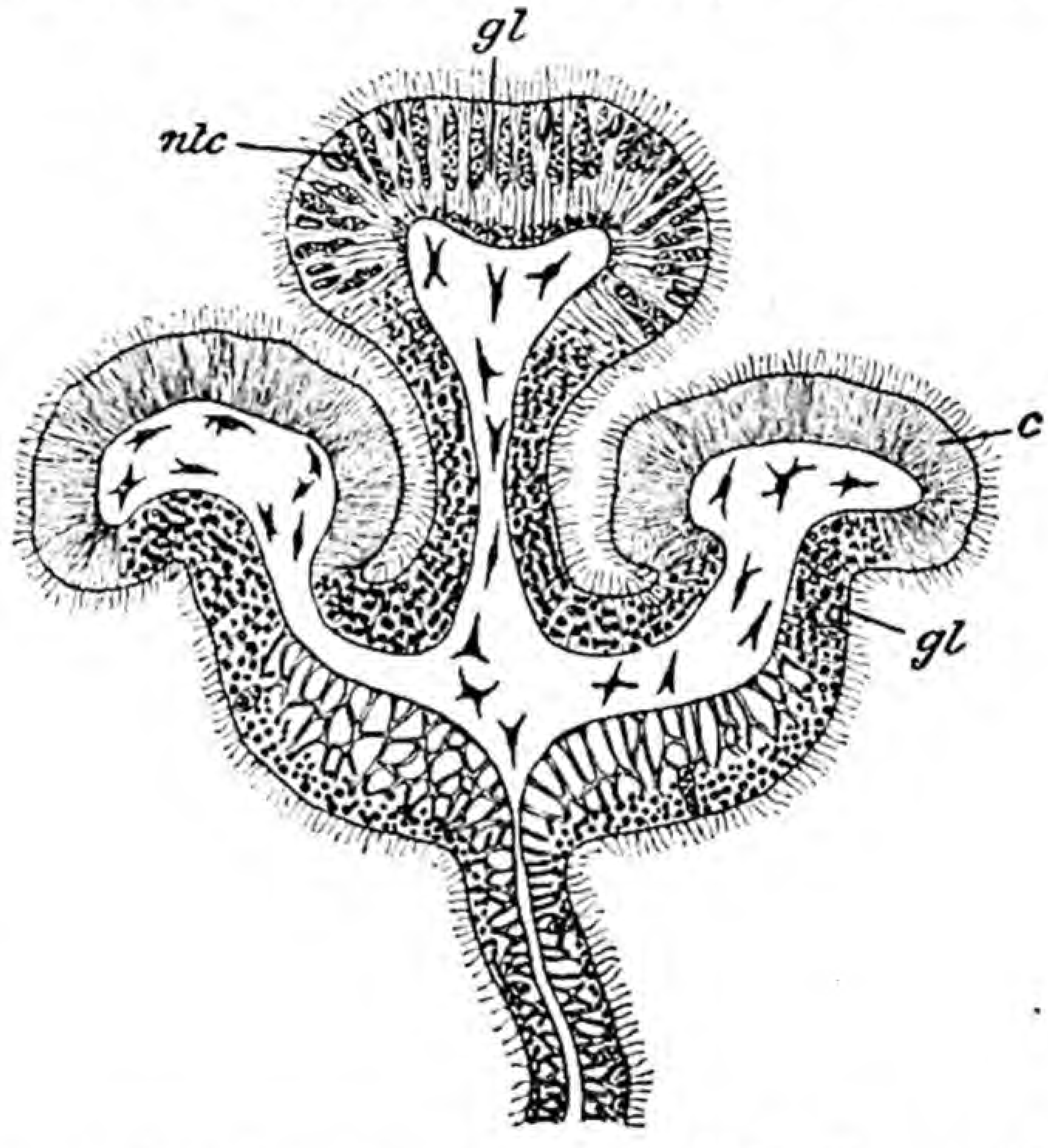


FIG. 144.—Transverse section of mesenteric filament of **Sagartia.** *c.* ciliated cells; *gl.* gland-cells; *ntc.* nematocysts. (After Hertwig.)

fibres, and partly of muscle-processes, like those of Hydra: the latter occur chiefly in the transverse muscular layer of the tentacles and are endodermal, the longitudinal layer is formed of distinct fibres of ectodermal origin: the great muscles of the mesenteries are of course endodermal. Although always derived either from the ectoderm or endoderm, many of the muscle-fibres of Urticina undergo a remarkable change of position by becoming sunk in the mesoglœa, and thus appearing to belong to that layer (Fig. 142, *l. m.*). This fact is significant from the circumstance that, as we shall see, the muscles of all animals above the Cœlenterata are mesodermal structures.

The **nervous system** is very simple. It consists of a layer of delicate fibres lying between the epithelial and muscular layers of the ectoderm. A similar

layer of nerve-fibres has been described to occupy a corresponding position in the endoderm. This layer is not indicated in Fig. 142. Among the fibres are found nerve-cells (Fig. 142, *nv.c.*), often of large size, and occurring chiefly in the disc and tentacles. Thus, as in the polype-forms previously described, the nervous system is a typical nerve-net, and shows no concentration into a definite central nervous system such as occurs in Medusæ.

Reproductive Organs.—Sea-anemones are diœcious, the sexes being lodged in distinct individuals. The gonads—ovaries or testes—are developed in the substance of the mesenteries (Fig. 140, *gon.*), a short distance from the edge, and, when mature, often form very noticeable structures. The reproductive products are obviously, as in the Scyphozoa, lodged in the endoderm. The sperms, when ripe, are discharged into the stomach and escape by the mouth : they are then carried, partly by their own movements, partly by ciliary action, down the gullet of a female, where they find their way to the ovaries and fertilize the eggs.

The **development** of Sea-anemones resembles, in its main features, that of the Scyphozoa. The fertilized ovum undergoes more or less regular division, the details differing considerably in individual cases, and becomes converted into a *planula*, an elongated ovoidal body with an outer layer of ciliated ectoderm and an inner layer of large endoderm cells, surrounding a closed enteric cavity, usually filled with a mass of yolk, which serves as a store of nutriment.

In this condition the embryo escapes from the parent, through the mouth, swims about for a time, and then settles down, becoming attached by its broader or anterior end. At the opposite or narrow end a pit appears, the rudiment of the stomodæum ; this deepens, and, its lower or blind end becoming perforated, effects a communication with the enteric cavity.

The mesenteries are developed in regular order, but in a way which would certainly not be suspected from their arrangement in the adult. First of all, a single pair of mesenteries (Fig. 145, *A*, *1*) grow from the body-wall to the gullet, being situated one on each side of the vertical plane, at right angles to the long diameter of the stomodæum, and near one end of that tube. The enteric cavity thus becomes divided into two chambers, a larger or *dorsal* and a smaller or *ventral*, and the embryo acquires a distinct bilateral symmetry. Next a pair of mesenteries (*2*) appear in the dorsal chamber, dividing it into a median and two lateral compartments; then a third pair (*3*) in the ventral chamber, producing a similar division; then a fourth pair (*4*) in the middle compartment of the dorsal chamber; then a fifth pair (*B*, *5*) in the lateral compartments of the dorsal chamber; and a sixth (*6*) in the lateral compartments of the ventral chamber. The order in which the mesenteries appear differs in the various Actinozoa. Thus the most common temporal sequence from dorsal to ventral is 2, 4, 1, 3, instead of 4, 2, 1, 3, as in our example (Fig. 145, *A*). Soon the longitudinal muscles are developed, and the fate of these primitive pairs of mesenteries can be seen. The third and fourth pairs become the two directive couples of the adult; another couple of primary mesenteries is constituted, on each side of the vertical plane, by one of the mesenteries of the first and one of the sixth pair; a third couple is similarly formed by a mesentery of the second and one of the fifth pair. Thus it is only in the case of the directive mesenteries that an adult couple coincides with an embryonic pair : in other instances the two mesenteries of a couple are of different orders, belonging to distinct embryonic pairs. The mesenteric filaments of the first cycle of mesenteries are partly ectodermal, partly endodermal in origin, those of the remainder entirely endodermal.

The tentacles are developed in a somewhat similar order to that of the development of the mesenteries. The first to make its appearance is connected with the larger or dorsal enteric chamber mentioned above: for some time it remains much longer than any of its successors, and thus accentuates in a marked degree the bilateral symmetry of the embryo.

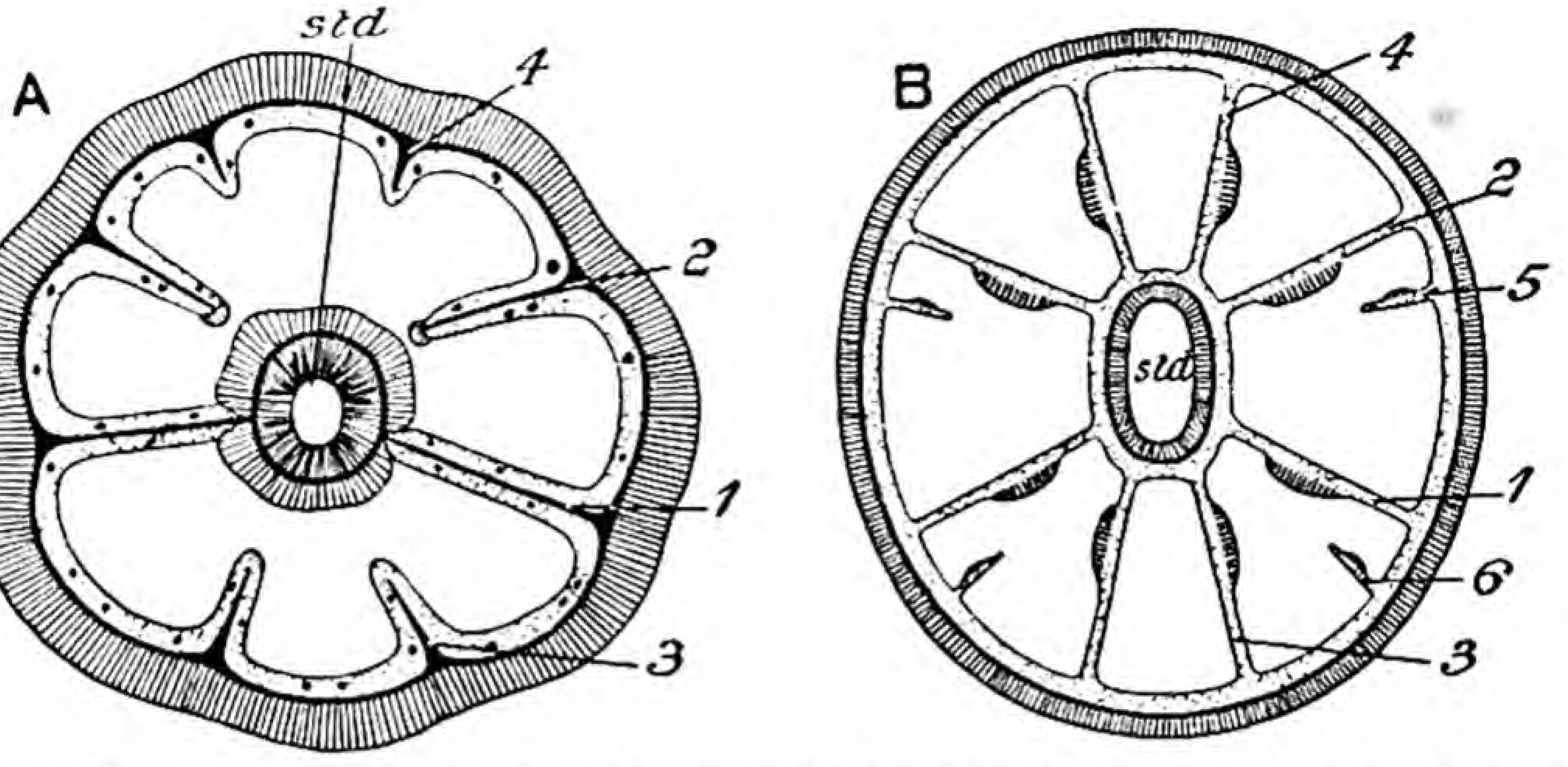


FIG. 145.—Transverse sections of early (*A*) and later (*B*) stages of an embryo Sea-anemone (**Actinia**). The mesenteries are numbered in the order of their development; *std.* stomodæum. (After Korschelt and Heider.)

It will be noticed that the development of the Sea-anemone is accompanied by a well-marked metamorphosis, but that there is no alternation of generations. In this respect its life-history offers a marked contrast with that of Obelia.

2. Distinctive Characters and Classification.

The Actinozoa are Cœlenterata which exist only in the polype-form, no medusa-stage being known in any member of the class. The actinozoan differs from the hydrozoan and scyphozoan polype mainly in possessing a stomodæum: it differs from the hydrozoan and many scyphozoan polypes in the possession of mesenteries or vertical radiating partitions, which extend inwards from the body-wall and some of which join the stomodæum. The free margins of the mesenteries bear coiled mesenteric filaments, which appear to answer to the gastric filaments of the Scyphozoa, but are partly ectodermal in origin. The mesenteries are developed in pairs, symmetrically on each side of a vertical plane: their final radial arrangement is secondary.

The body-wall consists of ectoderm and endoderm separated by a stout mesoglœa containing fibres and cells. The stomodæum consists of the same layers reversed—i.e., its lining membrane is ectodermal. The mesenteries are formed of a double layer of endoderm with a supporting plate of mesoglœa. Nematocysts, frequently of a more complex form than those of the Hydrozoa and Scyphozoa, are present in the tentacles, body-wall, stomodæum, and mesenteric filaments. The muscular system is well developed, and contains both ectodermal and endodermal fibres and endodermal muscle-processes. The nervous system is a typical nerve-net; there is no concentration of nervous elements to form a central nervous system.

The gonads are developed in the mesenteries, the sex-cells are lodged in the endoderm, and the ripe sexual products are discharged into the cœlenteron. The fertilized egg develops into a planula, which, after a short free existence, settles down and undergoes metamorphosis into the adult form. Except in one doubtful instance there is no alternation of generations.

In some Actinozoa the animal remains simple throughout life, but in most members of the class an extensive process of longitudinal fission takes place, the result being the formation of colonies of very various forms and often of great size. Budding and a kind of transverse fission recalling the strobilation in the Scyphozoa also occur. It is difficult, in many cases, to distinguish between incomplete longitudinal fission and budding. Some kinds, again, resemble Urticina in having no hard parts or skeletal structure of any kind ; but the majority possess a skeleton, formed either of carbonate of lime or of a horn-like or chitinoid material, and developed, in most cases though not in all, from the ectoderm.

The Actinozoa are classified as follows :—

Sub-Class I.—Hexacorallia.

Actinozoa in which the tentacles and mesenteries are usually very numerous and are frequently arranged in multiples of five or six. The tentacles are usually simple, unbranched, hollow cones. There are commonly two siphonoglyphes and two pairs of directive mesenteries : the remaining mesenteries are usually arranged in couples with the longitudinal muscles of each couple facing one another.

Order 1.—Actiniaria.

Hexacorallia which usually remain simple, but in a few instances form small colonies. The tentacles and mesenteries are numerous, and there is no skeleton. This order includes the Sea-anemones.

Examples : *Urticina* (Fig. 140), *Edwardsia* (Fig. 152), *Minyas* (Fig. 155), *Adamsia* (Fig. 160).

Order 2.—Madreporaria.

Hexacorallia which resemble the Actiniaria in the general structure of the soft parts, but which usually form colonies, and always possess an ectodermal calcareous skeleton. This order includes the vast majority of Stony Corals (Figs. 148, 149, and 159).

Order 3.—Zoantharia.

Solitary or colonial Hexacorallia with one ventral siphonoglyphe. The tentacles are unbranched. The body-wall is usually encrusted with foreign bodies of a calcareous nature. In a few cases there is a horny axial skeleton. The order comprises two families, the more important of which was formerly included amongst the Actiniaria (*Zoanthidæ*, Fig. 146).

Order 4.—Antipatharia.

Compound tree-like Hexacorallia in which the tentacles and mesenteries are comparatively few (6—24) in number. A skeleton is present in the form of a branched chitinoid axis, developed from the ectoderm, which extends throughout the colony. This order includes the "Black Corals" (Fig. 153).

Order 5.—Ceriantharia.

Solitary Hexacorallia with one dorsal siphonoglyphe. All mesenteries are complete. There are two kinds of tentacles: marginal and oral tentacles. The slightly pointed aboral end possesses a terminal porus (*Pachycerianthus*, Fig. 154).

Sub-Class II.—Octocorallia.

Actinozoa in which the tentacles and mesenteries are always eight in number. The tentacles are pinnate, *i.e.*, produced into symmetrical branchlets. There is never more than one siphonoglyphe, which is ventral in position, *i.e.*, faces the proximal end of the colony. The mesenteries are not arranged in couples, and their longitudinal muscles are all directed ventrally, *i.e.*, towards the same side as the siphonoglyphe.

Order 1.—Alcyonaria.

Octocorallia in which the skeleton usually consists of calcareous spicules or small irregular bodies occurring in the mesoglœa, but probably originating from wandering ectoderm cells. The common "Dead-men's fingers" (*Alcyonium*, Fig. 156) has a skeleton of this type. In some cases the spicules become aggregated so as to produce a coherent skeleton, which may form a branched axis to the whole colony, as in the precious Red Coral (*Corallium*, Fig. 148), or a series of connected tubes for the individual polypes, as in the Organ-pipe Coral (*Tubipora*, Fig. 151). In the "Blue Coral" (*Heliopora*) the skeleton is a massive structure resembling that of the Madreporaria. Most genera are compound; a few, such as *Hartea* (Fig. 147)—which, however, is probably a larval form—are simple.

Order 2.—Gorgonaria.

Compound tree-like Octocorallia, with a calcareous or horny skeleton of ectodermal origin forming a branched axis throughout the colony. Spicules are present in the mesoglœa. There is no siphonoglyphe. The beautiful "Sea-fans" belong to this group (Fig. 157).

Order 3.—Pennatularia.

Octocorallia in which the colony is usually elongated, and has one end embedded in the mud at the sea-bottom, while the opposite or distal end bears the polypes, usually on lateral branches. The stem is supported by a calcareous

or horny skeleton. The polypes are dimorphic. The "Sea-pens" (*Pennatula*) are the commonest members of this group (Fig. 150).

3. General Organization.

The chief variations in the **external form** of the Actinozoa are due to the diverse modes of budding: as we shall see, the structure of the individual polypes or zooids is remarkably uniform—at least as regards all the essentials of their organization.

Nearly all the Actiniaria or Sea-anemones are simple, and in the few instances where colonies are formed, these are usually small, and contain a very limited number of zooids. In *Zoanthus* (Fig. 146) the original polype sends out a horizontal branch or *stolon* (*st.*), from which new polypes arise.

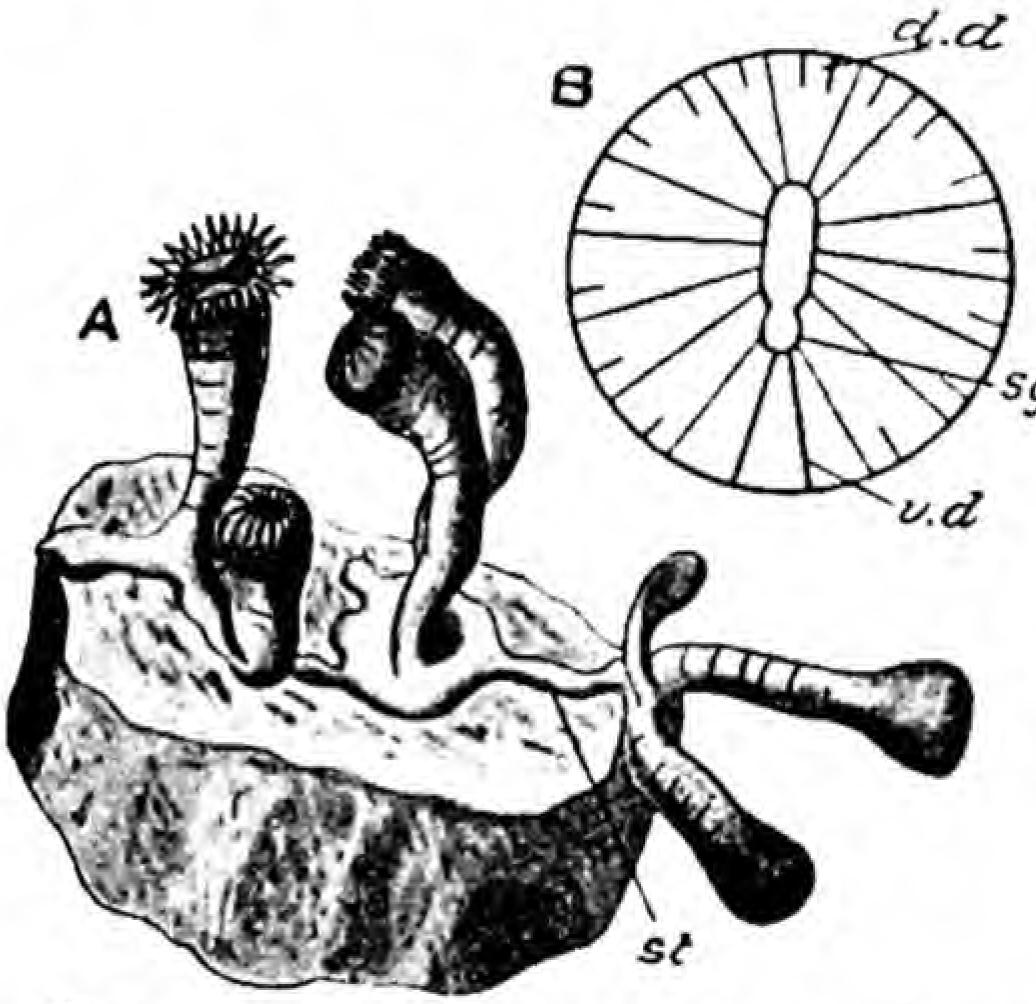


FIG. 146.—**Zoanthus sociatus.** *A*, entire colony; *st.* stolon. *B*, transverse section. *sgph.* siphonoglyphes; *d. d.* dorsal, and *v. d.* ventral directive mesenteries. (After McMurrich and Korschelt and Heider.)

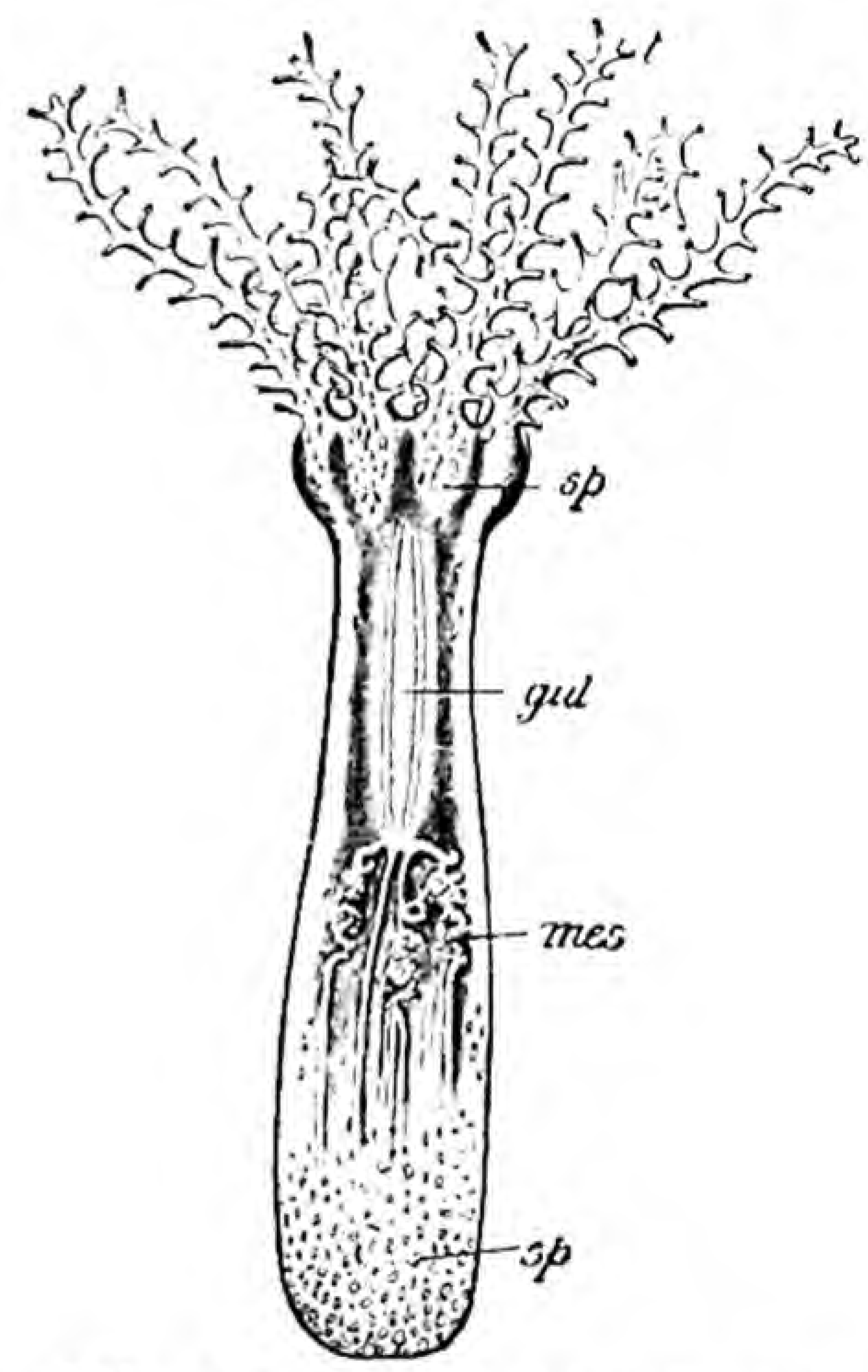


FIG. 147.—**Hartea elegans.** *gul.* gullet; *mes.* mesentery; *sp.* spicules; *t.* tentacles. (After Perceval Wright.)

Besides the Sea-anemones the only simple forms are certain Madreporarian corals, such as *Flabellum* (Fig. 158, *A*, *B*), and three genera of Alcyonaria, of which *Hartea* (Fig. 147) may be taken as an example.

The simplest mode of **budding** is that just described in Zoanthus, in which new zooids are developed from a narrow band-like or tubular stolon (Fig. 146, *st.*). A more usual method resembles that with which we are already familiar in the Hydrozoa, new buds being formed as lateral out-growths, and a tree-like colony arising with numerous zooids springing from a common stem or cœnosarc. Corallium and Gorgonia (Figs. 148 and 157) are good examples of this type of growth. In other cases the buds grow more or less parallel with one another, producing massive colonies either of close-set zooids or of zooids separated by

a solid cœnosarc. As examples of this type we may take *Palythoa*, the most complex of the Actiniaria, and many of the common Madreporaria, such as *Astræa* (Fig. 149). In the Sea-pens (*Pennatularia*) the proximal end of the elongated colony (Fig. 150) is sunk in the mud, and the distal end bears zooids springing either directly from the cœnosarc or, as in *Pennatula* itself, from flattened lateral branches. The stem itself is the equivalent of a polype.

FIG. 148.—**Corallium rubrum,** portion of a branch. (From Claus, after Lacaze-Duthiers.)

A very peculiar mode of budding occurs in the Organ-pipe Coral (*Tubipora*). The base of the original polype (Fig. 151) grows out into a flattened expansion from which new polypes arise, diverging slightly from one another as they grow, and separated by tolerably wide intervals. The distal ends of the polypes then grow out into horizontal expansions or *platforms* (*pl.*), formed at first of ectoderm and mesoglœa only, but finally receiving prolongations of the endoderm. The platforms extend, come in contact with one another, and fuse. In this way platforms of considerable extent are formed (*A*, *pl.*), uniting the polypes with one another. From the upper surfaces of the platforms, between the older polypes, new buds arise, and in this way the colony tends to assume the form of an inverted pyramid, the number of zooids, and consequently the diameter of the colony,

FIG. 149.—**Astræa pallida,** the living colony. (After Dana.)

increasing with the vertical growth of the latter. The skeleton of this remarkable coral will be referred to hereafter.

Although the general **structure of the individual polypes** of the Actinozoa is, as mentioned above, very uniform, the variations in detail are numerous and

interesting, especially among the Actiniaria. One of the most important points to consider is the *arrangement of the mesenteries*. In *Edwardsia* (Fig. 152), a genus which burrows in sand instead of attaching itself to rocks, etc., there are only eight mesenteries (*B*)—the usual two couples of directives, and two others on each side of the vertical plane, having their longitudinal muscles directed ventrally, and therefore not arranged in couples. The adult Edwardsia thus corresponds with a temporary stage in the development of one of the more typical Sea-anemones, viz., the stage with eight mesenteries shown in Fig. 145, *A*; it is probably to be looked upon as the most primitive or generalized member of the order. In *Zoanthus* (Fig. 146, *B*) the dorsal directives

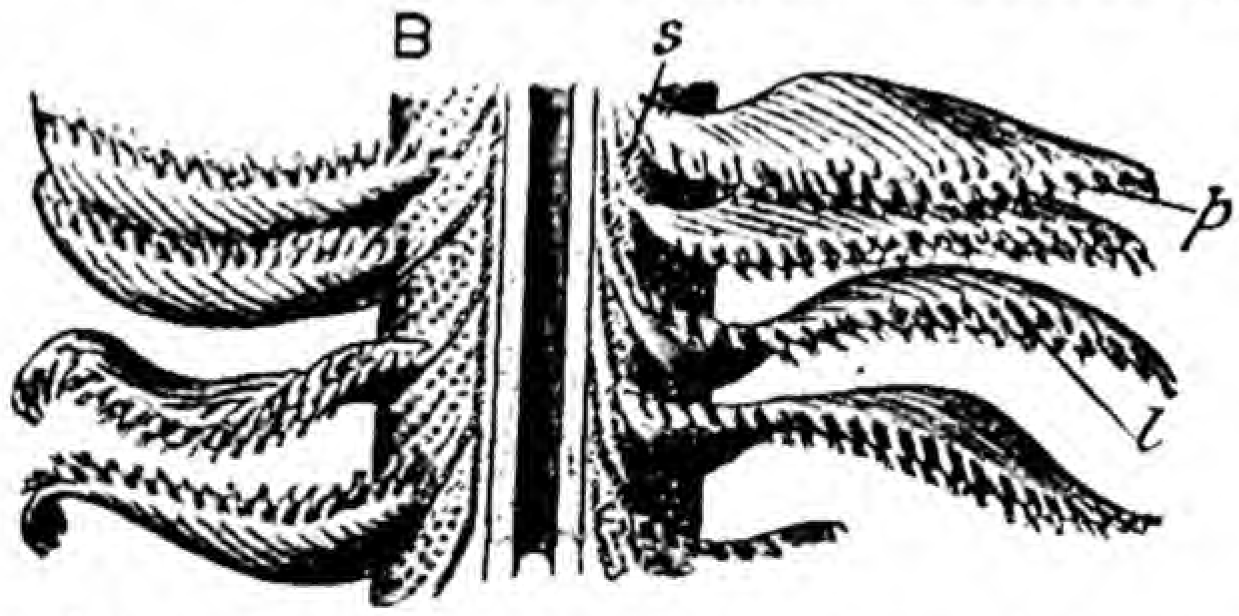


FIG. 150.—**Pennatula sulcata.** *A*, entire colony; *B*, portion of the same magnified. *l*. lateral branch; *p*. polype; *s*. siphonozooid. (After Koelliker.)

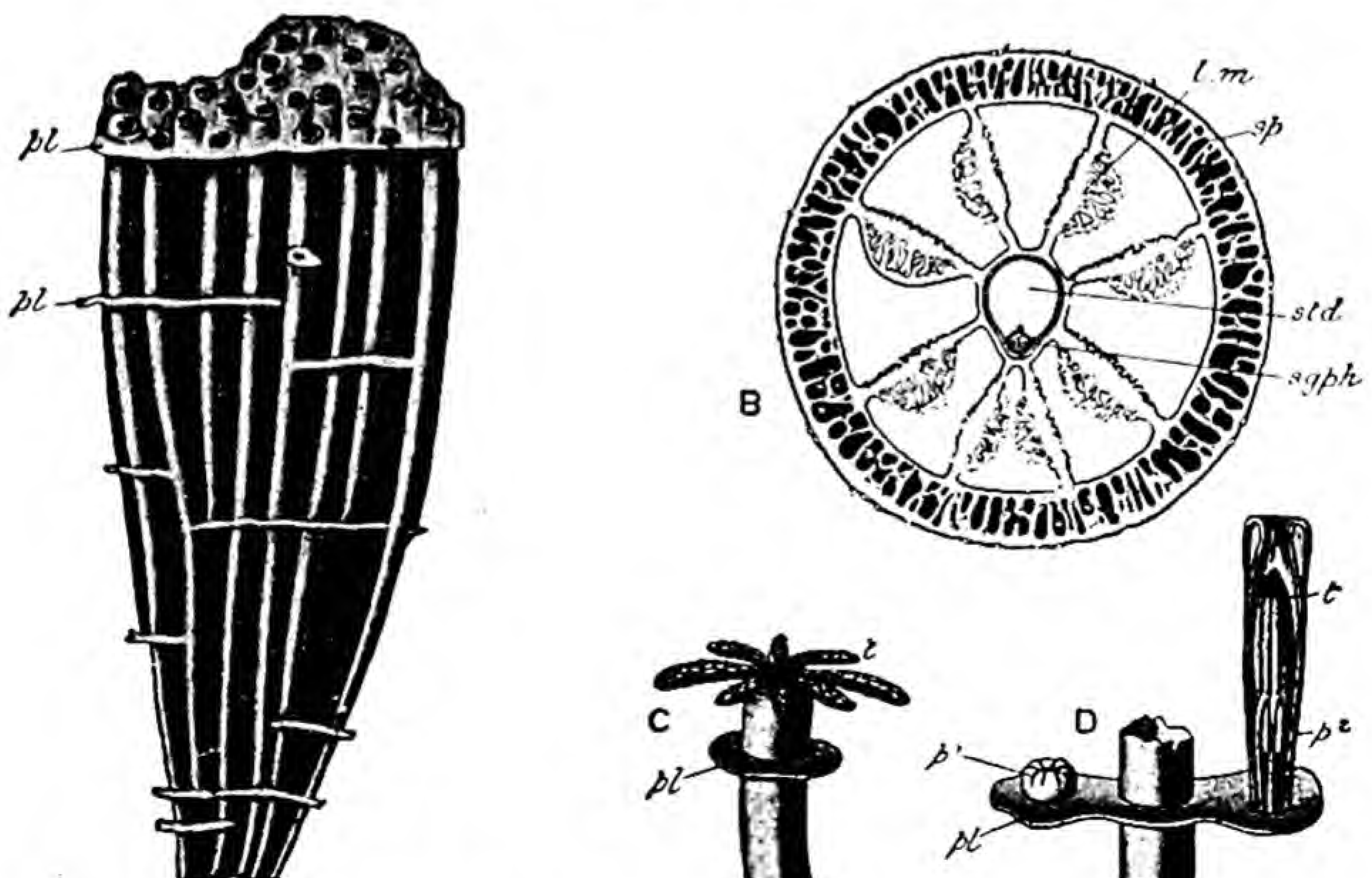


FIG. 151.—**Tubipora musica.** *A*, skeleton of entire colony; *B*, transverse sections of polype. *C*, single polype with tube and commencement of platform; *D*, growth of new polypes from platform. *l. m.* longitudinal muscles; *p*¹. *p*². polypes; *pl*. platform; *sgph*. siphonoglyphe; *sp*. spicules; *std*. stomodæum. (After Cuvier, Quoy and Gaimard, and Hickson.)

(*d. d.*) do not reach the gullet, and each lateral couple consists of one perfect and one small and imperfect mesentery. In Cerianthus, another burrowing form, there are a couple of very small ventral directives, and the remaining mesenteries are very numerous, not arranged in couples, and all directed ventrally at their outer ends, so as to have a very obviously bilateral arrangement : in this genus, as growth proceeds, new mesenteries are added on the dorsal side, and not, as is usual, between already formed couples. On the other hand, the genus *Gyractis* exhibits a perfectly radial arrangement : the mesenteries are all arranged in couples with the longitudinal muscles facing one another. Lastly, in all the more typical Sea-anemones there are either six, eight, or ten pairs of perfect mesenteries, which, as well as the secondary and tertiary cycles, are all arranged in couples, the longitudinal muscles of all but the one or two directive couples facing one another.

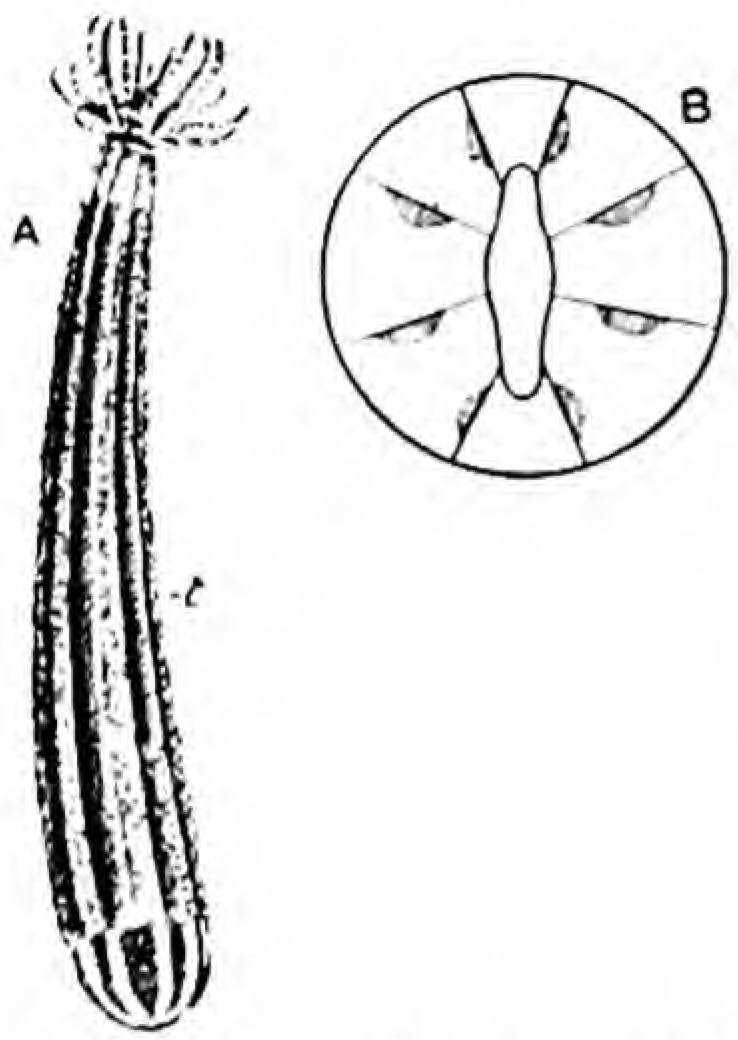


FIG. 152.—**Edwardsia claparèdii.** *A*, the entire animal; *t*, tube. *B*, transverse section. (After Andres, and Korschelt and Heider.)

In the Madreporaria the mesenteries are arranged, so far as is known, in the way just described for the typical Sea-anemones. In the Antipatharia there are six primary and sometimes either four or six secondary mesenteries. In the whole of the Octocorallia the mesenteries are eight in number : they are not arranged in couples, and their longitudinal muscles all face the same way, viz., towards the ventral aspect (Fig. 151, *B*). In this whole sub-class, therefore, the resemblance to Edwardsia is very close, the main difference being that the longitudinal muscles of the ventral directives face inwards in the Octocorallia, outwards in Edwardsia.

The **tentacles** in the Hexacorallia are usually very numerous, and in nearly

FIG. 153.—**Antipathes ternatensis,** portion of a branch, showing three zooids and the horny axis beset with spines. (From the *Cambridge Natural History*, after Schultze.)

all cases have the form of simple glove-finger-like out-pushings of the disc. In Edwardsia, however, they may be reduced to sixteen, and in some genera of Sea-anemones they are branched. In the Antipatharia (Fig. 153) they vary in number from six to twenty-four. When more than six are present, six of them are larger than the others.

In the Octocorallia, on the other hand, the tentacles, like the mesenteries,

are eight in number and are always pinnate, *i.e.*, slightly flattened and with a row of small branchlets along each edge (Fig. 147). Many Actiniaria have the tentacles perforated at the tip (Fig. 141, *A*, *p.*); and in some species these organs undergo degeneration, being reduced to apertures on the disc, which represent the terminal pores of the vanished tentacles and are called *stomidia*.

Many Sea-anemones possess curious organs of offence called *acontia* (Fig. 141, *A*, and Fig. 160, *ac.*). These are long delicate threads springing from the edges of the mesenteries: they are loaded with nematocysts, and can be protruded through minute apertures in the column, called "port-holes" or *cinclides* (*cn.*).

FIG. 154.—**Pachycerianthus multiplicatus.** (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co.), modified after Carlgren.)

Enteric System.—The *gullet* in the Actiniaria presents some remarkable modifications. It is usually a compressed tube with two siphonoglyphes. In *Gyractis* both grooves are absent and the tube itself is cylindrical with a circular mouth. In the *Zoantharia* the ventral gullet-groove is present (Fig. 146, *B*), and in the *Cerianthania* there is a dorsal syphonoglyphe only.

Fixed and Free Forms.—A large proportion of Actinozoa are permanently fixed, such, as for instance, most of the Stony Corals, the Sea-fans, Black Corals, etc. Most Sea-anemones are temporarily attached by the base, but are able slowly to change their position: some forms, such as *Edwardsia* (Fig. 152) and *Pachycerianthus* (Fig. 154) usually live partly buried in sand enclosed in a tube formed of discharged stinging-capsules, the oral end with its crown of tentacles alone being exposed: others, such as *Peachia*, live an actually free life, habitually lying on the sea-bottom with the longitudinal axis horizontal like that of a worm: a few, such as *Minyas* (Fig. 155), have the aboral end dilated into a sac containing air and serving as a float; by its means these animals can swim at the surface of the sea, and are thus, alone among the Actinozoa, pelagic.

FIG. 155.—**Minyas.** *f.* float. (After Andres.)

Dimorphism.—With the exception of one genus of Stony Corals, the Hexacorallia are all homomorphic, *i.e.*, there is no differentiation of the zooids of a colony. But in the Octocorallia dimorphism is common: the ordinary zooids or polypes are accompanied by smaller individuals, called *siphonozooids* (Fig. 150, *s.*), having no tentacles, longitudinal muscles, or gonads.

None of the Actiniaria have a true **skeleton**: in some, however, there is a thick cuticle, and several kinds enclose themselves in a more or less complete

tube (Fig. 152), which may be largely formed of discharged nematocysts. The simplest form of skeleton is found in the solitary Alcyonarian genus *Hartea* (Fig. 147), already referred to, in which minute irregular deposits of calcium carbonate, called *spicules* (*sp.*), are deposited in the mesoglœa. A similar *spicular skeleton* occurs in the "Dead-men's finger" (Alcyonium, Fig. 156), where spicules of varying form are found distributed throughout the mesoglœa of the cœnosarc. In *Tubipora* (Fig. 151), the "Organ-pipe Coral," the mesoglœal spicules become closely fitted together, and form a continuous tube for each polype, the tubes being united by horizontal calcareous platforms (*pl.*) formed by deposits of spicules in the expansions already referred to. The skeleton of Tubipora is, therefore, an internal skeleton, and in the living state is covered by ectoderm. In the Red Coral of commerce (*Corallium*, Fig. 148) the originally separate spicules are embedded in a cement-like deposit of carbonate of lime, the result being the production of an extremely hard and dense branched rod, which extends as an axis through the cœnosarc. In the Blue Coral (*Heliopora*), on the other hand, the stony calcareous skeleton is not made up of fused spicules, but is solid from the first.

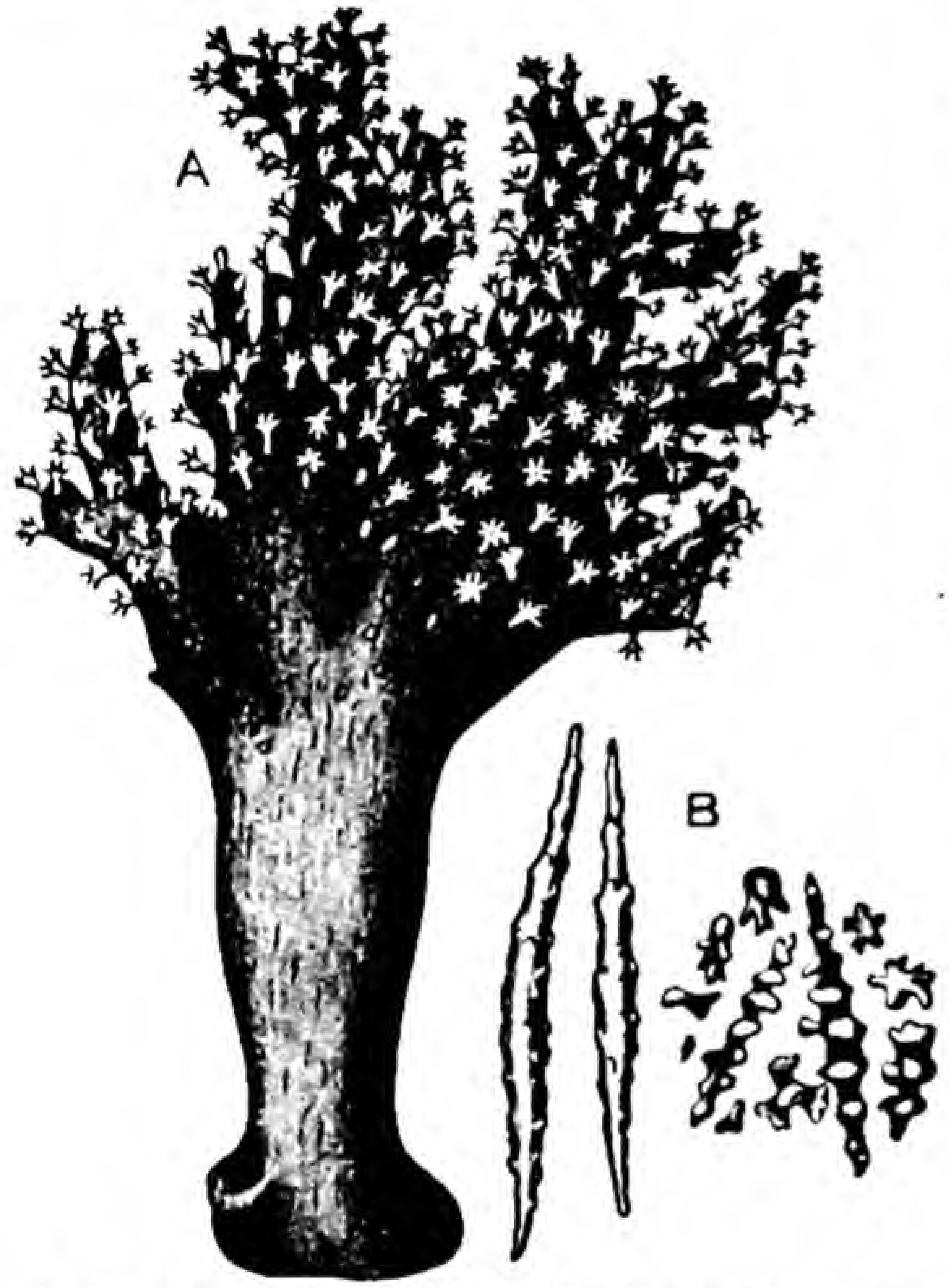


FIG. 156.—**Alcyonium palmatum**, *A*, entire colony; *B*, spicules. (After Cuvier.)

Another type of skeleton is found in the Antipatharia (Fig. 153) and in the Gorgonaria (Fig. 157). It also consists of an axial rod, extending all through the colony and branching with it, but is formed of a flexible horn-like material. Moreover, it is not mesoglœal, but ectodermal in origin: in close contact with it is an epithelium, from the cells of which it is produced as a cuticular secretion, and this epithelium is formed as an invagination of the base of the colony. In addition to its axis, Gorgonia contains numerous spicules in the mesoglœa of the cœnosarc. In some of the Gorgonaria the axial skeleton is partly horny, partly calcareous.

In the Sea-pen (*Pennatula*, Fig. 150) and its allies the stem of the colony is supported by a horny or calcareous axis which is unbranched, not extending into the lateral branches. In this case the axis is contained in a closed cavity lined by an epithelium, the origin of which is still uncertain. Spicules occur

in the mesoglœa, some of them microscopic, others readily visible to the naked eye.

In the Madreporaria we have a skeleton of an entirely different type, consisting, in fact, of a more or less cup-like calcareous structure, secreted from the ectoderm of the base and column of the polype. When formed by a solitary polype, such a "cup-coral" is known as a *corallite*: in the majority of species

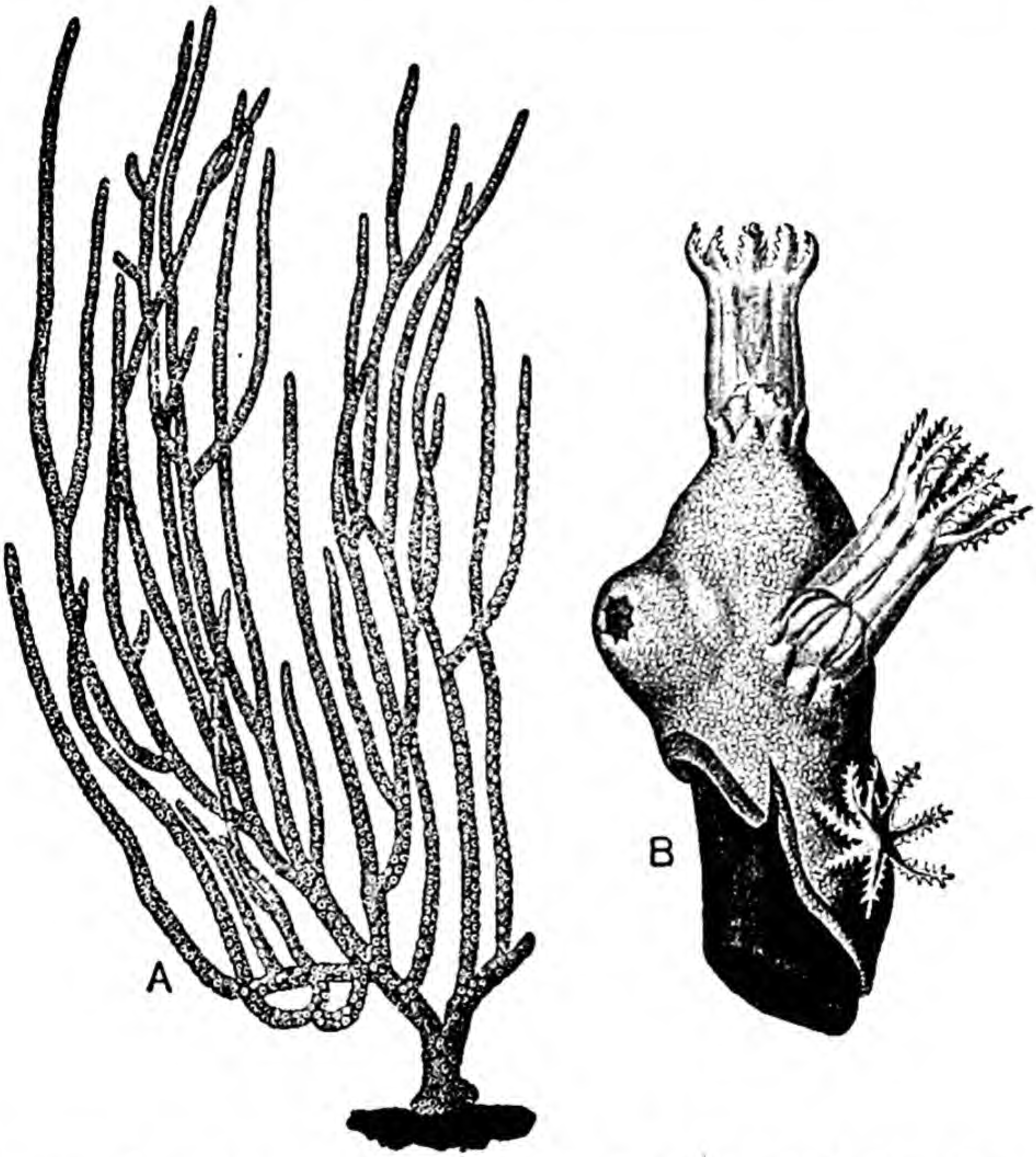


FIG. 157.—**Gorgonia verrucosa.** *A*, entire colony; *B*, portion of the same magnified. (After Koch and Cuvier.)

a large number—sometimes many thousands—of corallites combine to form a *corallum*, the skeleton of an entire coral-colony.

The structure of a corallite is conveniently illustrated by that of the solitary genus *Flabellum* (Fig. 158, *A*, *B*). It has the form of a short conical cup, much compressed so as to be oval in section. Its wall or *theca* (*th.*) is formed of dense stony calcium carbonate, white and smooth inside, rough and of a brownish colour outside, except towards the margin, where it is white. Its aboral

end is produced into a short stalk or *peduncle*, by which the Coral is attached in the young state, becoming free when adult: in many other simple Corals there is no stalk, but attachment to the support is effected by means of a flattened *basal plate* (*C*, *b. pl.*). From the inner surface of the theca a number of radiating partitions, the *septa* (*sep.*), proceed inwards or towards the axis of the cup, and, like the mesenteries of a polype, are of several orders,

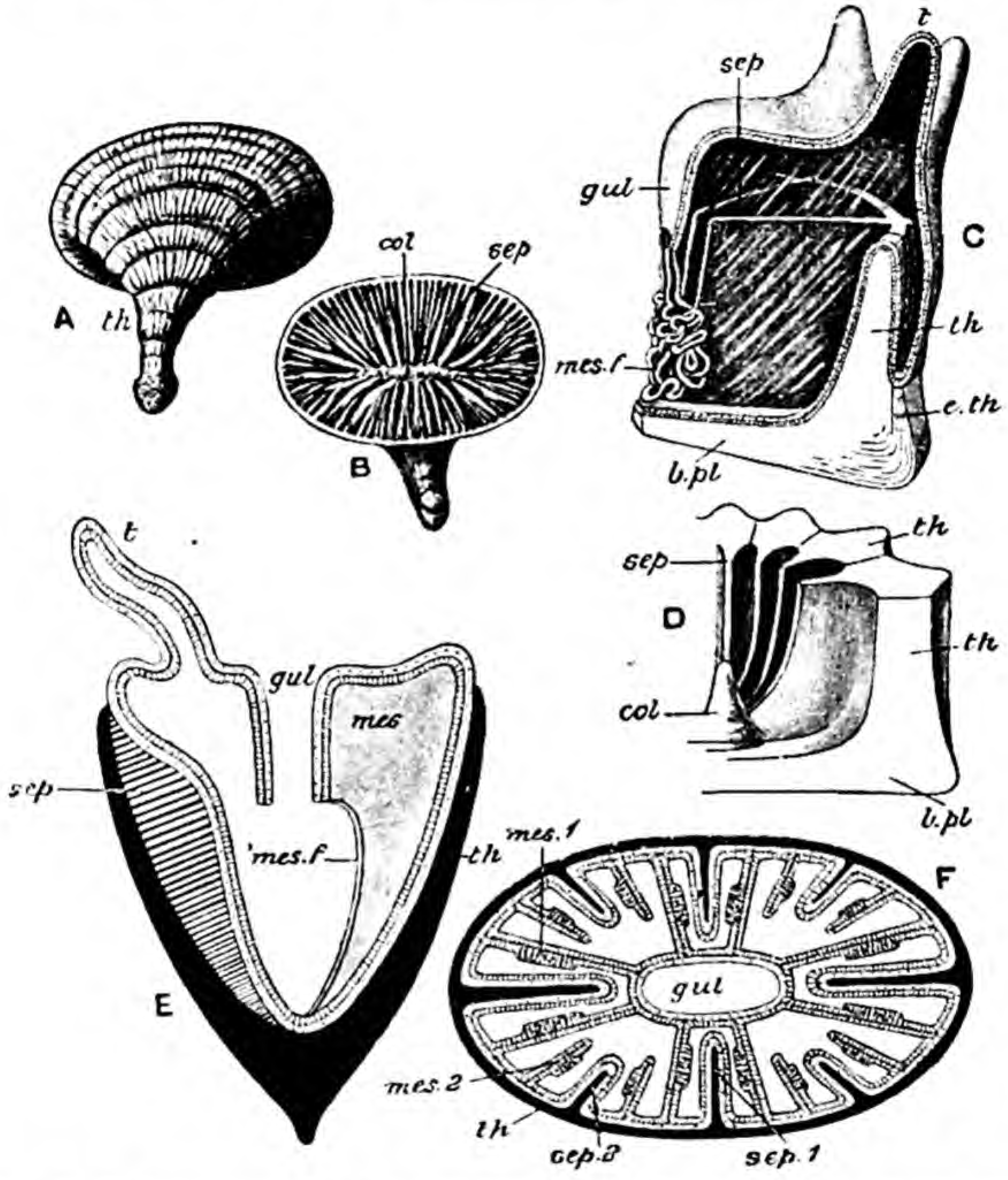


FIG. 158.—*A*, *B*, two views of **Flabellum curvatum.** *C*, semi-diagrammatic view of a simple coral; *D*, portion of a corallite; *E*, *F*, diagram of a simple coral in longitudinal and transverse section; ectoderm dotted, endoderm striated, skeleton black. *b. pl.* basal plate; *col.* columella; *e. th.* epitheca; *gul.* gullet; *mes*, *mes. 1*, *mes. 2*, mesenteries; *mes. f.* mesenteric filaments; *sep.* septa; *t.* tentacle; *th.* theca. (*A* and *B* after Moseley; *C* and *D* after Gilbert Bourne.)

those extending furthest towards the centre being called primary septa, the others secondary, tertiary, and so on. Towards the bottom of the cup the primary septa meet in the middle to form an irregular central mass, the *columella* (*col.*). In some Corals the columella is an independent pillar-like structure arising from the basal plate (*D*, *col.*).

In many Corals there is a distinct calcareous layer investing the proximal

portion of the theca, and called the *epitheca* (*C*, *e.th.*). Some species have the inner portions of the septa detached so as to form a circlet of narrow upright columns, the *pali*. In others there are horizontal partitions or *dissepiments* passing from septum to septum, and in others, again, complete partitions or *tabulæ*, like those of Millepora (p. 150), extending across the whole corallite. In the Mushroom-coral (*Fungia*) the corallite is discoid, the theca is confined to the lower surface, and small calcareous rods, the *synapticula*, connect the septa with one another.

In the living condition the polype fills the whole interior of the corallite and projects beyond its edge to a greater or less degree according to its state of expansion (*C*). The proximal part of the body-wall is thus in contact with the theca, which has the relation of a cuticle, and is, in fact, a product of the ectoderm. The free portion of the body-wall is frequently, in the extended state, folded down over the edge of the theca so as to cover its distal portion. The septa alternate with the mesenteries, each lying in the space between the two mesenteries of one couple, and each being invested by an in-turned portion of the body-wall (*E*, *F*). Thus the septa, which appear at first sight to be internal structures, are really external: they lie altogether outside the enteric cavity, and are in contact throughout with ectoderm.

The ectodermal nature of the entire corallite is further proved by its development. The first part to appear is a ring-shaped deposit of carbonate of lime between the base of the polype and the body to which it adheres: sections show this ring to be formed by the ectoderm cells of the base. The ring is soon converted into a disc, the *basal plate*, from the upper surfaces of which a number of ridges arise, arrayed in a star-like fashion: these are the rudiments of the septa. Here, again, sections show that each septum corresponds with a radial in-pushing of the base, and is formed as a secretion of the invaginated ectoderm. As the septa grow they unite with one another at their outer ends, and thus form the theca. In some cases, however, the theca appears to be an independent structure.

The almost infinite variety in form of the compound Corals is due, in the main, to the various methods of budding, a subject which has already been referred to in treating of the actinozoan colony as a whole. According to the mode of budding, massive Corals are produced in which the corallites are in close contact with one another, as in Astræa (Fig. 149); or tree-like forms, such as Dendrophyllia (Fig. 159, *A*), in which a common calcareous stem, the *cœnenchyma*, is formed by calcification of the cœnosarc (*cs.*), and gives origin to the individual corallites. It is by this last-named method, the cœnosarc attaining great dimensions and the individual corallites being small and very numerous, that the most complex of all Corals, the Madrepores (*Madrepora*, Fig. 159, *B*) are produced.

The microscopic structure of corals presents two main varieties. In what

are called the *aporose* or poreless corals, such as Flabellum, Astræa, etc., the various parts of the corallite are solid and stony, while in the *perforate* forms, such as Madrepora, all parts both of the corallites and of the connecting cœnenchyma have the characters of a mesh-work, consisting of delicate strands of carbonate of lime united with one another in such a way as to leave interstices, which in the living state are traversed by a network of interlacing tubes, representing the cœnosarc, and placing the polypes of the colony in communication.

The Blue Coral (*Heliopora*), one of the Alcyonaria, has a massive corallum of the same general appearance as a Madreporarian. The lobed surface bears

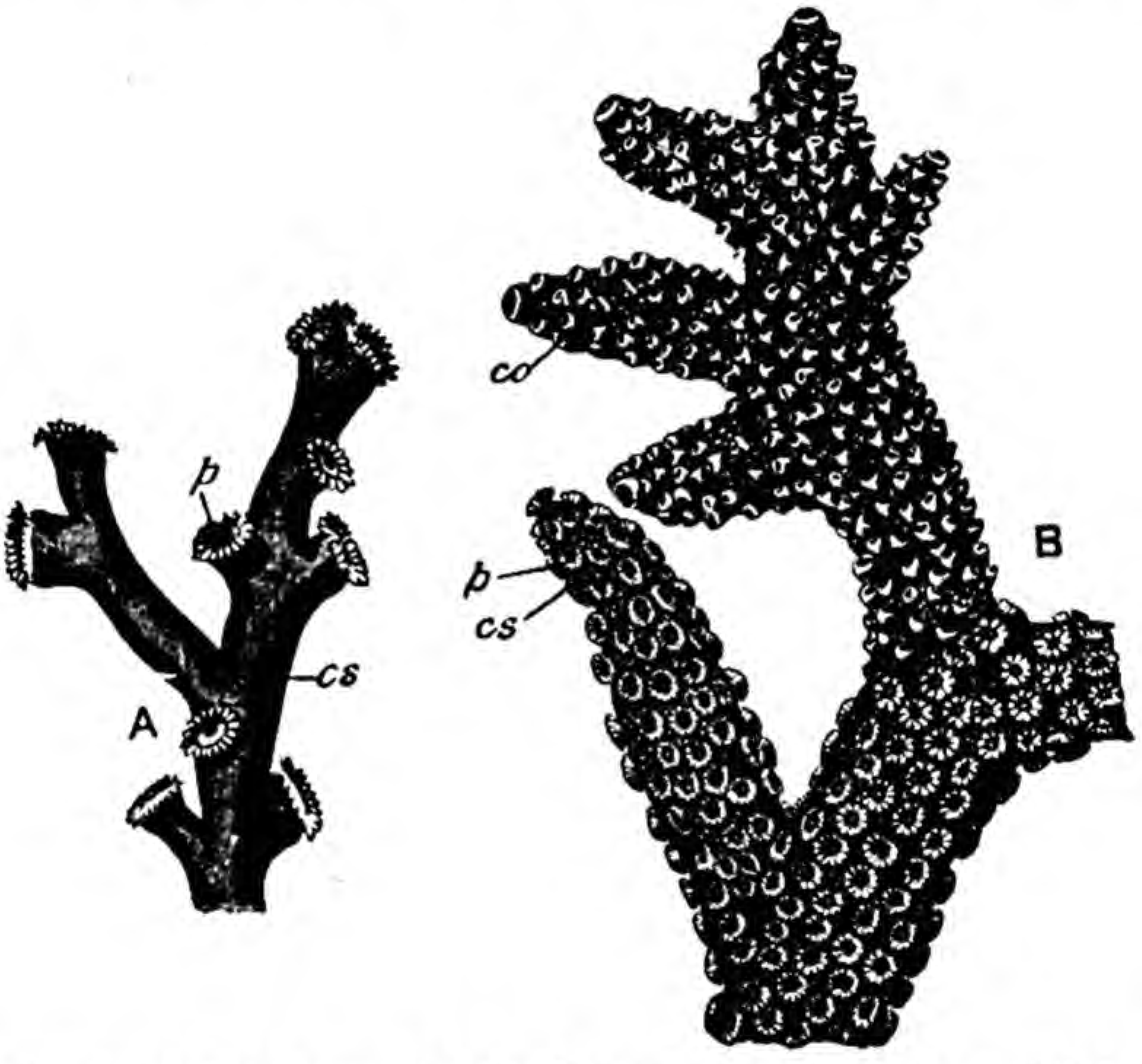


FIG. 159.—*A*, **Dendrophyllia nigrescans,** *B*, **Madrepora aspera.** *co.* corallites; *cs.* cœnosarc; *p.* polypes. (After Dana.)

apertures of two sizes, the larger being for the exit of the ordinary polypes, the smaller for the siphonozooids. Tabulæ are present, and septum-like ridges, which, however, have no definite relations to the mesenteries and are inconstant in number.

Colour.—The Actinozoa are remarkable for the variety and brilliancy of their colour during life. Everyone must have noticed the vivid and varied tints of Sea-anemones; but most dwellers in temperate regions get into the habit of thinking of Corals as white, and have no conception of their marvellously varied and gorgeous colouring during life. The Madrepores, for instance, may be pink, yellow, green, brown, or purple; Tubipora has green polypes, contrasting strongly with its crimson skeleton; and the effect of the bright

red axis of Corallium is greatly heightened by its pure white polypes. In Heliopora the whole coral is bright blue; the tropical Alcyonidæ are remarkable for their elaborate patterns and gorgeous coloration; and Pennatula, in addition to its vivid colours, is phosphorescent.

In most cases the significance of these colours is quite unknown. In some species, however, "yellow cells" or symbiotic Algæ have been found in the endoderm, where they probably serve the same purpose as the similar structures which we have already studied in Radiolaria.

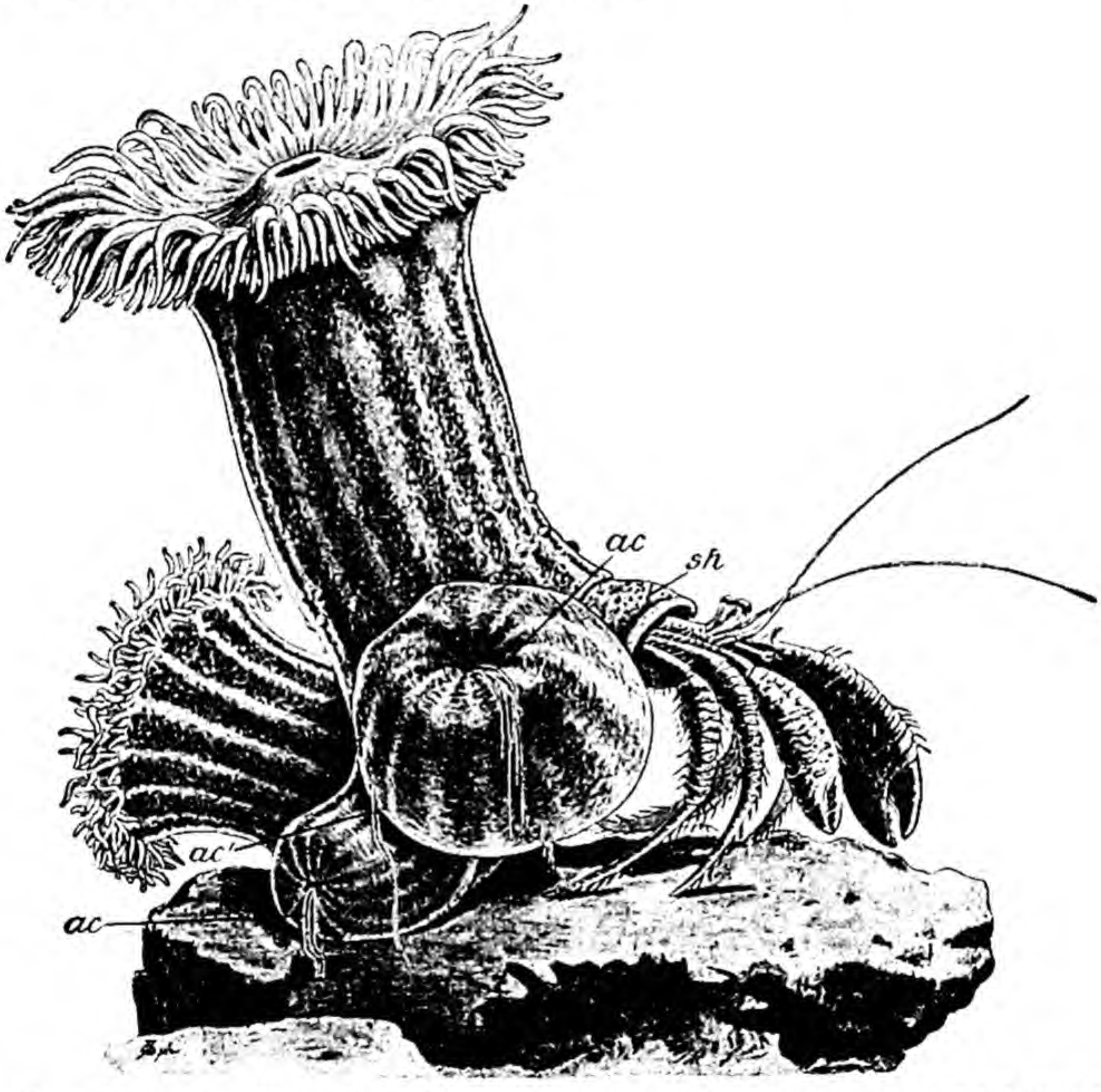


FIG. 160.—**Adamsia palliata,** four individuals attached to a Gastropod shell inhabited by a Hermit-crab. *ac. ac'.* acontia; *sh.* shell of Gastropod. (After Andres.)

Many Actinozoa, like many sponges, furnish examples of **commensalism,** a term used for mutually beneficial association of two organisms of a less intimate nature than occurs in symbiosis. An interesting example is furnished by various Sea-anemones (Fig. 160) which live on *Gastropod* shells inhabited by Hermit-crabs. The Sea-anemone is carried from place to place by the Hermit-crab, and in this way secures a more varied and abundant food-supply than would fall to its lot if it remained in one place. On the other hand, the Hermit-crab is protected from the attack of predaceous Fishes by retreating into its

shell and leaving exposed the Sea-anemone, which, owing to its toughness, and to the pain caused by its poisonous stinging-capsules, is usually avoided as an article of food. Species of *Peachia*, which in the adult state burrow in sand, in a larval condition live as parasites or commensals in the radial canals of Scyphomedusæ.

Other Sea-anemones—such as the gigantic *Discosoma* of the Great Barrier Reef—are found associated with small Fishes or Crustacea, which have their abode in the enteric cavity. In this case the Fish secures shelter in a place where it is very unlikely to be disturbed, and the two animals are strictly commensals or " mess-mates " since they share a common table. A somewhat similar instance is furnished by the Blue Coral (Heliopora), already referred to more than once. The corallum contains not only the apertures for the polypes and siphonozooids, but also tubular cavities of an intermediate size, in each of which is found a small chætopod Worm, belonging to the genus *Leucodore*. As the polypes are frequently found retracted at a time when the Worms are protruded from their holes in search of food, it is not surprising that the latter should have been credited with the fabrication of the coral. *Trapezia*, a genus of Crabs, always lives in interstices of a particular species of Madrepore.

The **distribution** of the Actiniaria is world-wide, and in many cases the same genera are found in widely separated parts of the world. They are, however, larger, and of more varied form and colour in tropical regions, for instance on coral-reefs. The largest reef-anemone, *Discosoma*, found also in the Mediterranean, attains a diameter of 2 feet. Most members of the order are littoral, living either between tide-marks or at slight depths, but a few are pelagic, and several species have been dredged from depths of from 10 to 2900 fathoms.

The Madreporaria, taken as a whole, have also a wide distribution; but the number of forms in temperate regions is small, and the majority—including the whole of what are called reef-building Corals—are confined to the tropical parts of the Atlantic, Indian, and Pacific Oceans, flourishing only where the lowest winter temperature does not sink below 68° F. (20° C.). Thus their northernmost limits are the Bermudas in the Atlantic, and Southern Japan in the Pacific; their southernmost limits, Rio and St. Helena in the Atlantic, Queensland and Easter Island in the Pacific: in other words, they extend to about 30° on each side of the equator. Moreover, they have a curiously limited bathymetrical distribution, flourishing only from high-water mark down to a depth of about 20 fathoms, but not lower.

Many of the Pacific Islands are formed entirely of coral rock, others are fringed with reefs of the same, and the whole east coast of Northern Queensland is bounded, for a distance of 1250 miles, by the Great Barrier Reef, a line of coral rock more or less parallel to and at a distance of from 10 to 90 miles from the land. Such reefs consist of gigantic masses of coral rock fringed

by living coral, the latter growing upon a basis of dead coral, the interstices of which have been filled up with *débris* of various kinds, so as to convert the whole into a dense limestone.

The Antipatharia and many of the Octocorallia, such as the Gorgonaria and Pennatularia, have also a world-wide distribution, and, even in temperate regions, Black Corals and Sea-fans may attain a great size: the members of both these groups, as well as the Sea-pens, are found at moderate depths. The Red Coral is found only in the Mediterranean, at a depth of 10 to 30 fathoms, and at the Cape Verde Islands: other species of Corallium occur on the coast of Japan, at Mauritius and Madeira. Tubipora and Heliopora have the same distribution as the reef-building Corals.

From the palæontological point of view, corals are of great importance; they are known in the fossil condition from the Ordovician epoch upwards and in many formations occur in vast quantities, forming what are called coral limestones. The majority of fossil forms are referable to existing families, but in the Palæozoic era the dominant group was the *Rugosa*, the affinities of which are still very obscure. In these the corallites are usually bilaterally symmetrical, the septa are arranged in multiples of four, and the cup often presents on one side a pit, the *fossula*, where at least one septum is generally reduced.

SUB-PHYLUM ACNIDARIA

CLASS I.—CTENOPHORA.

1. Example of the Class—*Hormiphora plumosa*.

External Characters.—Hormiphora is a pear-shaped organism about 5–20 mm. in diameter, and of glassy transparency (Figs. 161 and 162). The species *H. plumosa* is found in the Mediterranean; allied forms belonging either to the same genus or to the closely allied genus *Pleurobrachia* are common pelagic forms all over the world.

From opposite sides of the broad end depend two long *tentacles* (*t.*), provided with numerous little tag-like processes, and springing each from a deep cavity or *sheath*, into which it can be completely retracted (Fig. 162, *t. sh.*). At the narrow end—where the stalk of a pear would be inserted—is a slit-like aperture, the *mouth* (*mth.*): this end is therefore oral. At the opposite or aboral pole is a slight depression, in which lies a prominent *sense-organ* (*s.o.*), to be described hereafter.

But the most striking and characteristic feature in the external structure of Hormiphora is the presence of eight equidistant meridional bands (*s.pl.*) starting from near the aboral pole, and extending about two-thirds of the distance towards the oral pole. Each band is constituted by a row of transversely arranged comb-like structures, consisting of narrow plates frayed at

their outer ends. During life the frayed ends are in constant movement, lashing to and fro, and so propelling the animal through the water. The *combs* are, in fact, rows of immense cilia, fused at their proximal ends : their presence and mode of occurrence—arranged in meridional *comb-ribs*, *costæ*, or *swimming-plates*—are strictly characteristic of the class, and indeed give it its name.

It will be seen at once that—apart from all considerations of internal structure—Hormiphora presents a similar combination of radial with bilateral symmetry as in some Hydrozoa, such as Ctenaria (Fig. 113, *I*), and as in the majority of the Actinozoa. The swimming-plates are radially arranged, and mark the eight adradii, but the slit-like mouth and the two tentacles indicate a very marked and characteristic bilateral symmetry. An imaginary line passing from the middle of the mouth to the sense-organ is the *primary axis*. A

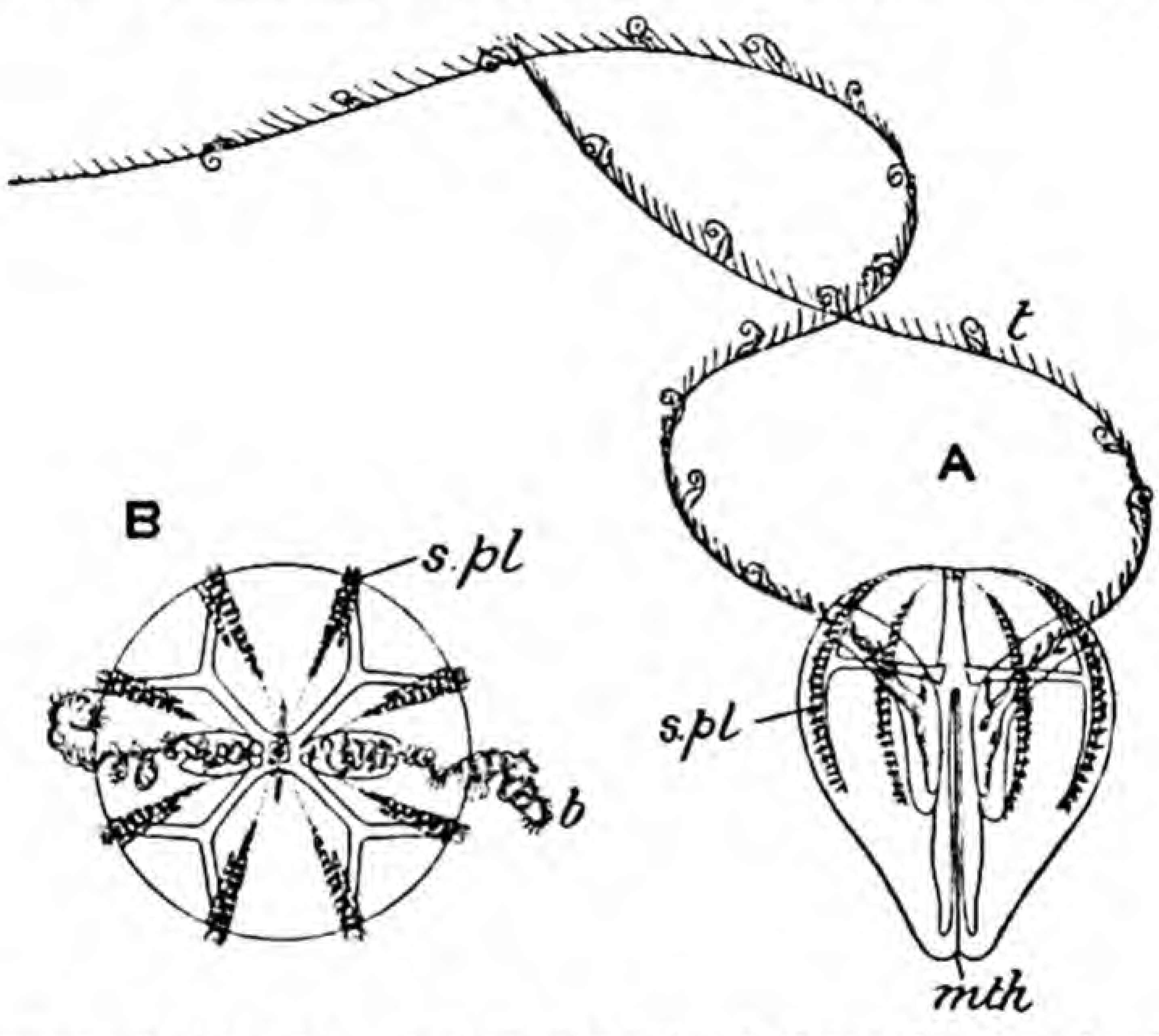


FIG. 161.—**Hormiphora plumosa.** *A*, from the side, *B*, from the aboral pole. *mth*. mouth ; *s. pl*. swimming plates ; *t*. and *b*. tentacles. (After Chun.)

plane passing through the longitudinal axis of the body, parallel with the long axis of the mouth, is called, as in the Actinozoa, the *vertical* or *sagittal plane* : it includes two per-radii, which are respectively dorsal and ventral. A plane at right angles to this, passing through both tentacles, and including right and left per-radii, is called the *transverse* or *lateral plane*. It is along these two planes alone that the body is capable of division into approximately equal halves.

Enteric System.—The mouth leads into a flattened tube (Fig. 162, *std*.), often called the stomach, but more correctly the gullet or *stomodæum*. It reaches about two-thirds of the way towards the aboral pole, and its walls are produced internally into ridges (*std. r*.), which increase the area for the absorption of digested food. Living prey is seized by the tentacles, ingested

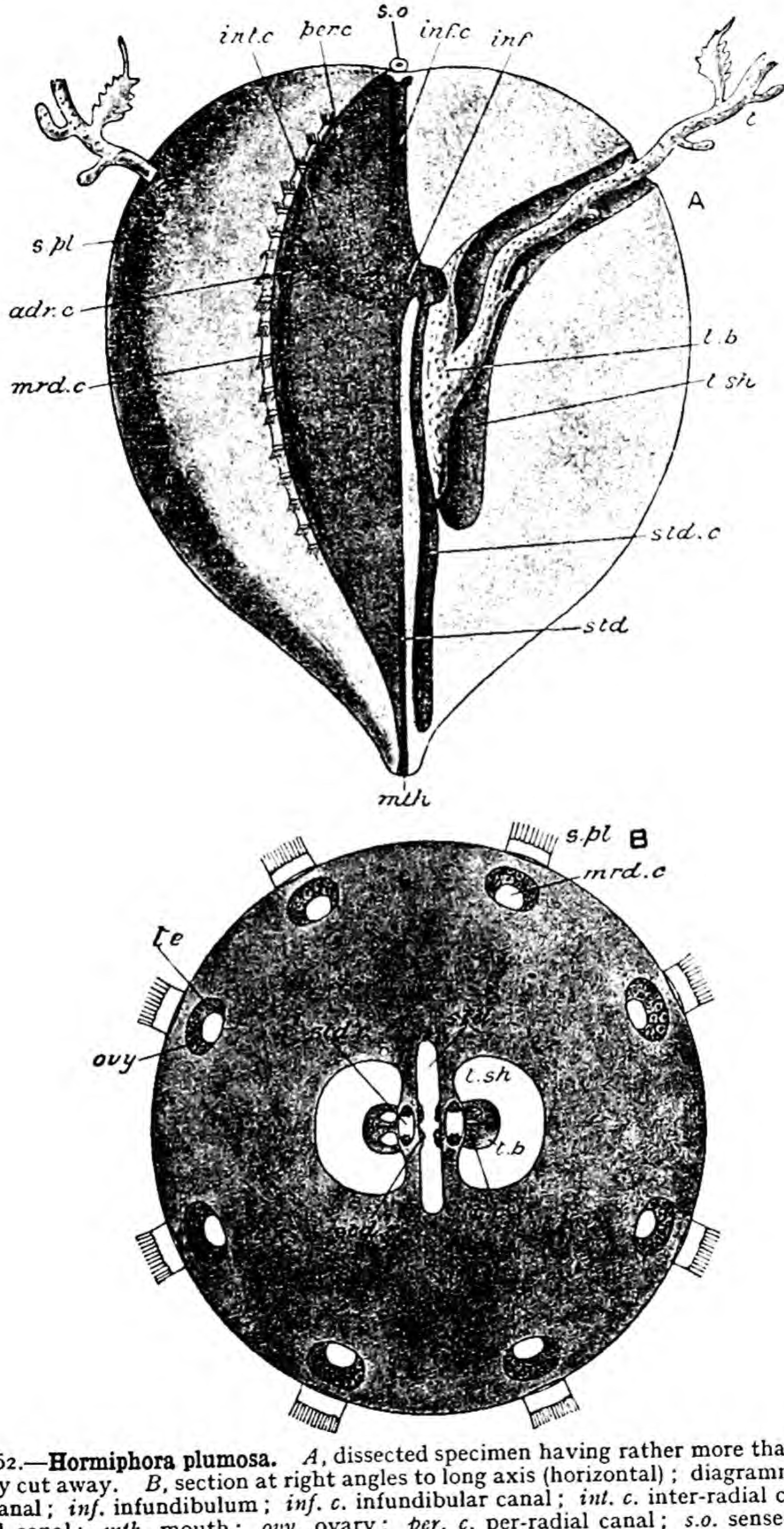


FIG. 162.—**Hormiphora plumosa.** *A*, dissected specimen having rather more than one quarter of the body cut away. *B*, section at right angles to long axis (horizontal); diagrammatic. *adr. c.* adradial canal; *inf.* infundibulum; *inf. c.* infundibular canal; *int. c.* inter-radial canal; *mrd. c.* meridional canal; *mth.* mouth; *ovy.* ovary; *per. c.* per-radial canal; *s.o.* sense-organ; *s.pl.* swimming-plates; *std.* stomodæum; *std. c.* stomodæal canal; *std. r.* stomodæal ridges; *t* tentacle; *t. b.* base of tentacle; *t. c.* tentacular canal; *te.* testis; *t. sh.* tentacular sheath.

by the aid of the mobile edges of the mouth, and digested in the stomodæum, which is thus physiologically, though not morphologically, a stomach. The products of digestion make their way into the various parts of the canal-system, presently to be described, and indigestible matters are passed out at the mouth.

Towards its upper or aboral end the stomodæum gradually narrows and opens into a cavity called the *infundibulum* (*inf.*), which probably answers to the stomach of an Actinozoon or a medusa, and is flattened in a direction at right angles to the stomodæum—*i.e.*, in the transverse plane. From the infundibulum three tubes are given off: one, the *infundibular canal* (*inf. c.*), passes directly upwards, and immediately beneath the aboral pole divides into four short branches, two of which open on the exterior by minute apertures, the *excretory pores* (Fig. 163, *A*, *ex. p.*). The two other canals given off from the infundibulum are the *per-radial canals* (*per. c.*): they pass directly outwards, in the transverse plane, and each divides into two *inter-radial canals* (*int. c.*), which in their turn divide each into two *adradial canals* (*adr. c.*). These successive bifurcations of the canal-system all take place in a horizontal plane (Fig. 163, *B*), and each of the ultimate branches or adradial canals opens into a *meridional canal* (*mrd. c.*), which extends upwards and downwards beneath the corresponding swimming-plate. Furthermore, each per-radial canal gives off a *stomodæal canal* (*std. c.*), which passes downwards, parallel to and in close contact with the stomodæum, and a *tentacular canal* (*t. c.*), which extends outwards and downwards into the base of the corresponding tentacle. Each tentacle presents a thickened *base* (*t. b.*), closely attached to the wall of the sheath, and giving off a long flexible filament, beset with processes of two kinds—one simple and colourless, the other leaf-like, beset with branchlets, and of a yellow colour.

Cell-layers.—The body is covered externally by a delicate ectodermal epithelium (Fig. 163), the cells from which the combs arise being particularly large. The epithelium of the stomodæum is found by development to be ectodermal, that of the infundibulum and its canals endodermal: both are ciliated. The interval between the external ectoderm and the canal-system is filled by a soft jelly-like mesoglœa. The tentacle-sheath is an invagination of the ectoderm, and the tentacle itself is covered by a layer of ectoderm, within which is a core or axis formed by a strong bundle of longitudinal muscular fibres, which, as we shall see (p. 205), are of mesodermal origin, and which serve to retract the tentacle into its sheath.

Delicate muscle-fibres lie beneath the external epithelium and beneath the epithelium of the canal-system, and also traverse the mesoglœa in various directions. The feeble development of the muscular system is, of course, correlated with the fact that the swimming-plates are the main organs of progression, the Ctenophora differing from all other Cœlenterata in retaining cilia as locomotory organs throughout life.

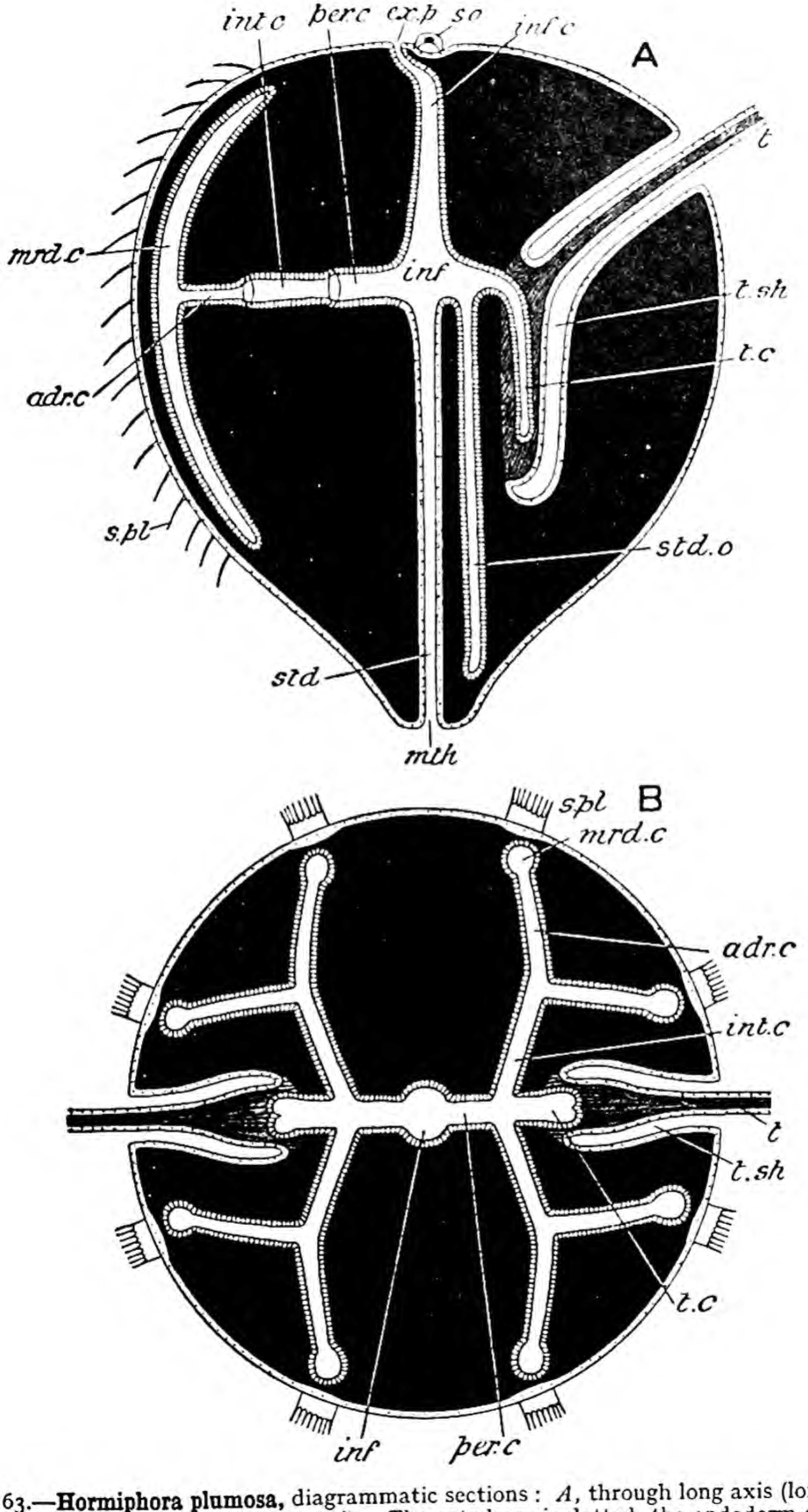


FIG. 163.—**Hormiphora plumosa,** diagrammatic sections : *A*, through long axis (longitudinal) ; *B*, at right angles to long axis (horizontal). The ectoderm is dotted, the endoderm striated, the mesoglœa black, and the muscular axis of the tentacles grey. Lettering as in Fig. 162, except *ex. p.* excretory pore.

A further striking difference between our present type and the Cœlenterata previously studied is the absence, in Hormiphora, of stinging-capsules. It is this absence of stinging capsules (*cnidoblasts*) to which the sub-phylum *Acnidaria* owes its name. The place of the stinging-capsules is taken, in a sense, by the peculiar **adhesive-cells** with which the branches of the tentacles

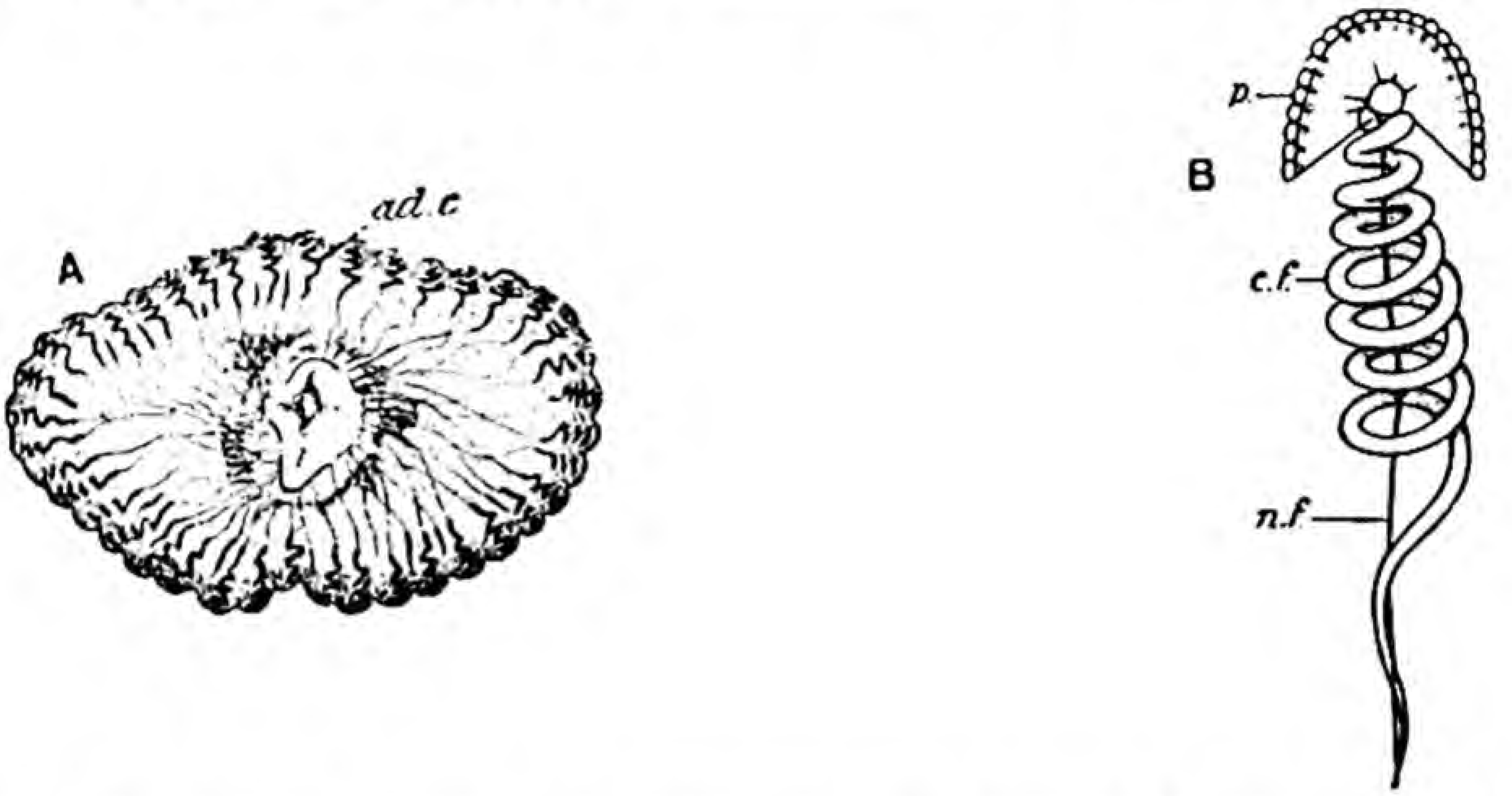


FIG. 164.—**Hormiphora plumosa.** *A*, transverse section of one of the branches of a tentacle; *B*, adhesive cell highly magnified. *ad. c.* adhesive cell; *c. f.* coiled filament; *n. f.* straight nuclear filament; *p.* papillæ. (After Hertwig and Taku Komai.)

are covered. An adhesive-cell (Fig. 164, *B*) has a convex surface, produced into small papillæ (*p.*), which readily adheres to any object with which it comes in contact and is with difficulty separated. In the interior of the cell is a spirally coiled filament (*c. f.*), the delicate inner end of which can be traced to the muscular axis of the tentacular branch. These spiral threads act as

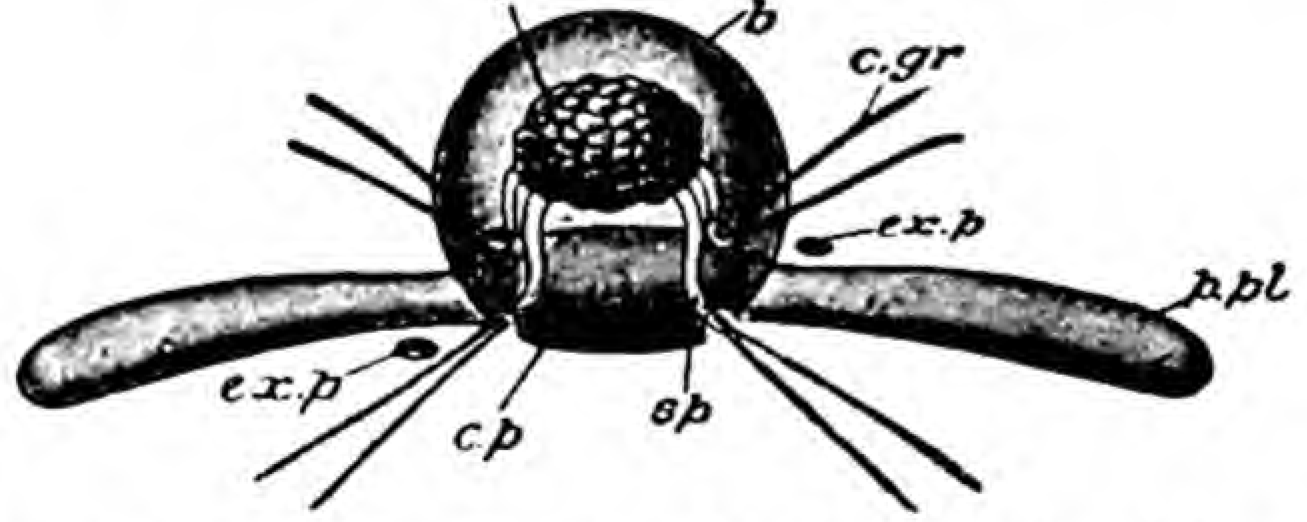


FIG. 165.—**Hormiphora plumosa,** Sense-organ. *b.* bell; *c. p.* ciliated plate; *c. gr.* ciliated groove; *ex. p.* excretory pore; *l.* calcareous particles; *p. pl.* polar plate; *sp.* spring. (Modified from Chun.)

springs, and tend to prevent the adhesive-cells being torn away by the struggles of the captured prey. A second filament which is straight represents the modified nucleus of the cell (*n. f.*).

The principal **sense-organ** is a peculiar apparatus situated, as already mentioned, at the aboral pole. In this region is a shallow depression (Fig. 165, *c. p.*) lined by ciliated epithelium and produced in the transverse plane into

two narrow ciliated areas, the *polar plates* (*p. pl.*). From the depression arise four equidistant groups of very large S-shaped cilia (*sp.*), united to form as many *springs* (*sp.*), which support a mass of calcareous particles (*l.*). From each spring a pair of *ciliated grooves* (*c. gr.*) proceeds outwards, and passes to the two swimming-plates of the corresponding quadrant. The calcareous mass, with its springs, is enclosed in a transparent case or *bell* (*b.*), formed of coalesced cilia. It appears that the whole apparatus acts as a kind of steering-gear, or apparatus for the maintenance of equilibrium. Any inclination of the long axis must cause the calcareous mass to bear more heavily upon one or other of the springs: the stimulus appears to be transmitted by the corresponding ciliated groove to a swimming-plate, and results in a vigorous movement of the combs. A sub-epithelial plexus of nerve-fibres with nerve-cells extends all over the surface of the body, and nerve-elements are also traceable in the mesoglœa.

Reproductive organs.—The animal is hermaphrodite, the organs of both sexes being found in the same individual. The *gonads* are developed in the meridional canals (Fig. 162, *B*), each of which has an ovary (*ovy.*) extending along the whole length of one side, a testis (*te.*) along the whole length of the opposite side. The organs are so arranged that in adjacent canals those of the same sex face one another. It will be seen that the reproductive products have, as in Scyphozoa and Actinozoa, the position of endoderm-cells: whether they are developed, in the first instance, from that layer is uncertain. When ripe, the ova and sperms are discharged into the canals, make their way to the infundibulum, thence to the stomodæum, and finally escape by the mouth. Fertilization takes place in the water.

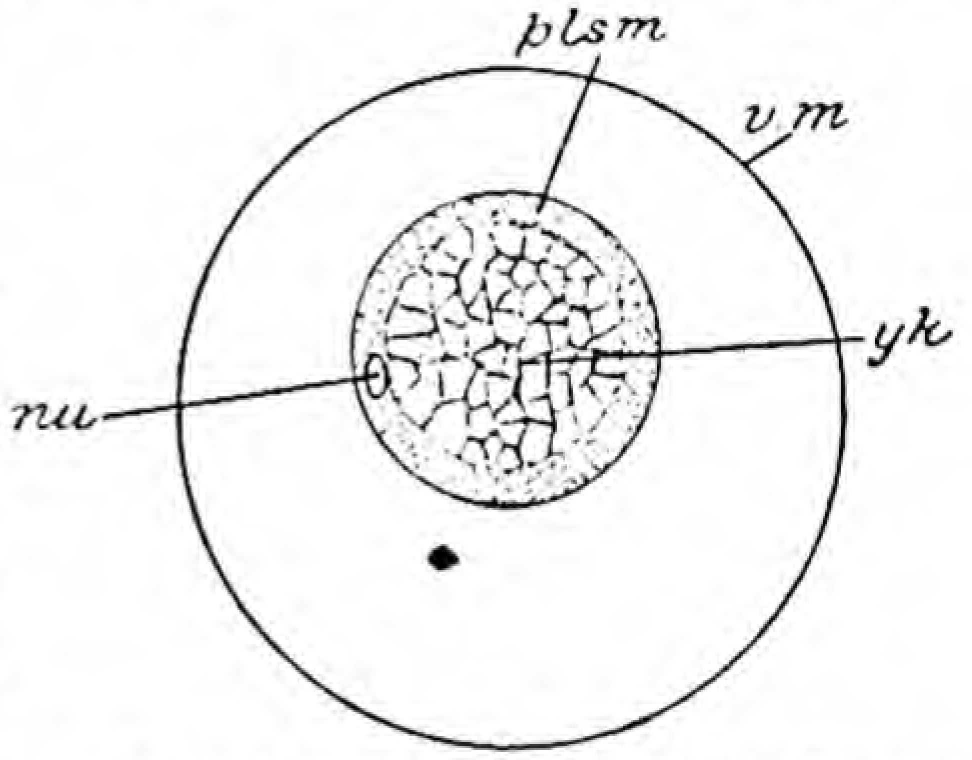


FIG. 166.—Ovum of **Eulampetia.** *nu.* nucleus; *plsm.* protoplasm; *v. m.* vitelline membrane; *yk.* yolk. (After Chun.)

Development.—The process of development has been traced in several genera closely allied to Hormiphora, so that there is every reason to believe that, in all essential particulars, the following description will apply to that genus.

The egg (Fig. 166) consists of an outer layer of protoplasm (*plsm.*) containing the nucleus (*nu.*), and of an internal mass of a frothy or vacuolated nature (*yk.*): the vacuoles contain a homogeneous substance which serves as a store of nutriment to the growing embryo, and apparently corresponds with the *yolk* which we shall find to occur in a large proportion of animal eggs. Enclosing the egg is a thin *vitelline membrane* (*v. m.*), separated from the protoplasm by a considerable space, filled with a clear jelly.

After fertilization the zygote undergoes cleavage, but the details of the process are very different from those we are familiar with in the other

Cœlenterata. The protoplasmic layer accumulates on the side which will become dorsal, and the zygote divides along a vertical plane, forming two cells each with a sort of protoplasmic cap. A second division takes place at right angles to the first, producing a four-celled stage, and each of the four cells divides again into daughter-cells of unequal size, the result being an eight-celled embryo, each cell with a protoplasmic cap at its dorsal end (Fig. 167,

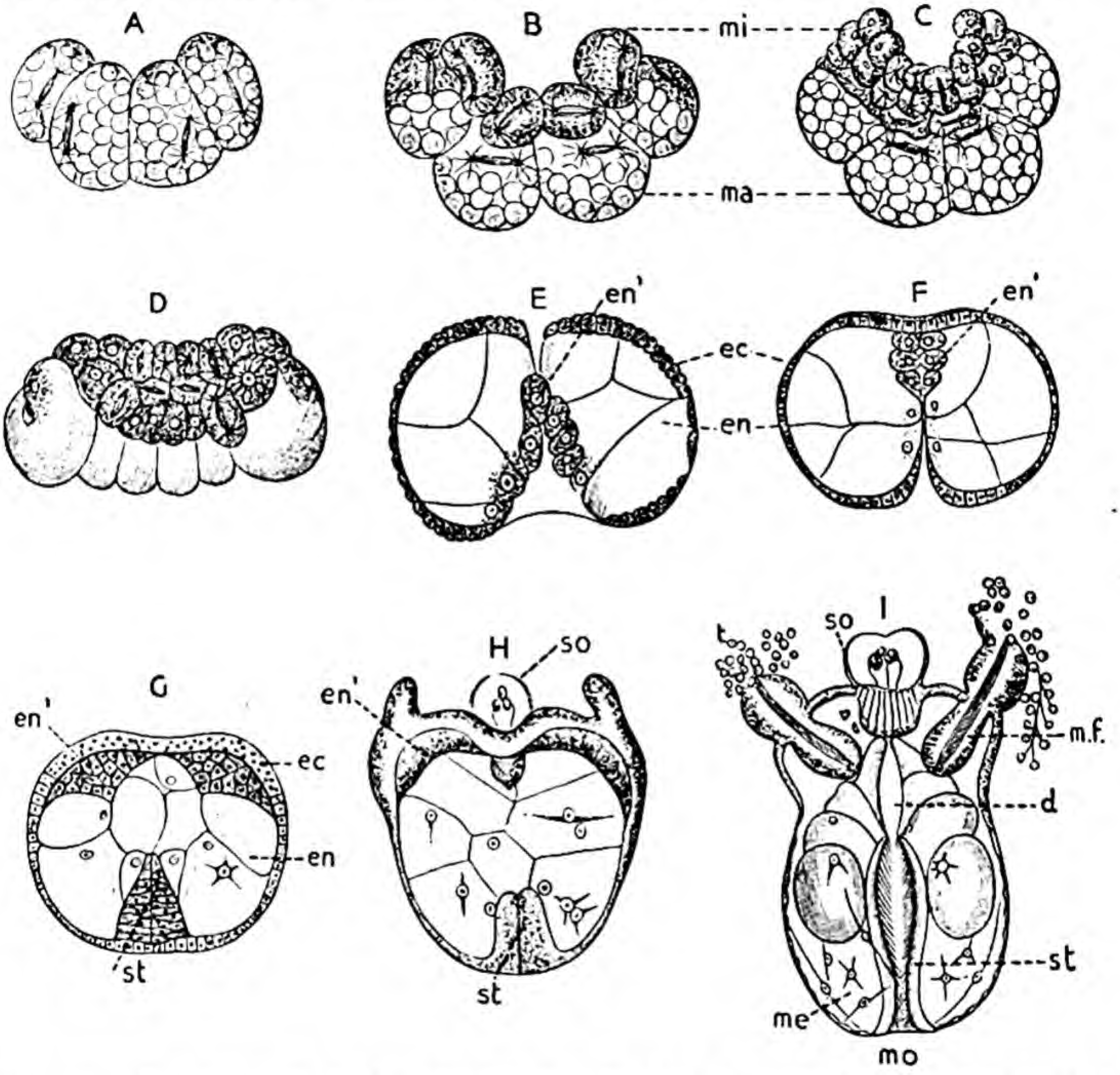


FIG. 167.—Development of **Callianira bialata.** In *A–D* only one half of the cleaving egg is seen. *d*, infundibulum; *ec*. ectoderm; *en*. endoderm; *en'*. small cells derived from endoderm; *ma*. macromeres; *me*. mesoglœa; *mi*. micromeres; *mo*. mouth; *m. f*. muscle fibres; *st*. stomodæum; *s. o*. sense-organ; *t*. tentacle. (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co., Ltd.), after Metschnikoff.)

A). Next a horizontal division takes place, dividing off the protoplasmic caps as distinct cells, and so producing a sixteen-celled stage (*B*) in which we can distinguish eight large, ventral, yolk-containing cells or *macromeres* (*ma*.), and eight small, dorsal, protoplasmic cells or *micromeres* (*mi*.).

The micromeres increase rapidly in number by division, and are further added to by new small cells being budded off from the macromeres (*C*, *D*).

The result of this increase is that the micromeres gradually overspread the macromeres, the final result being the production of an embryo consisting of a central mass of large yolk-containing cells (*en.*) partly surrounded by an epithelium-like layer, incomplete below, of small cells (*ec.*). This stage corresponds with the gastrula of preceding types, the micromeres forming the ectoderm, the macromeres the endoderm, and the ventral edge of the ectodermal investment representing the blastopore. There is, however, no archenteron or gastrula-cavity, and the stage has been produced, not by a process of invagination or tucking-in, but by one of *epiboly* or overgrowth. A gap which is left between the ectoderm cells at the upper (aboral) pole—the *pseudoblastopore*—soon closes up (*E, F*).

The endoderm-cells increase in number, and become much elongated and arranged obliquely, their long axes radiating upwards and outwards, from the long axis of the entire embryo. Their lower (ventral) ends then become divided off, forming a number of small cells (*E, en'.*). A kind of invagination and rotation of the macromeres then takes place, resulting in the shifting of these small cells towards the upper pole (*F*). They mainly give rise to the tentacular canals. At the same time the ectoderm cells bounding the aperture of the invagination cavity grow into it so as to line its ventral portion: in this way the stomodæum (*G, H, I, st.*) is produced. The remainder of the cavity widens out and becomes the definite infundibulum (*I, d.*), and before long sends off four adradial pouches, the rudiments of the canal-system. At the same time the gelatinous mesoglœa (*me.*) makes its appearance between the ectoderm and endoderm, its cells being derived from ectoderm cells which migrate inwards, chiefly in the neighbourhood of the stomodæum.

The later processes of development may be described very briefly. The canal-system gradually assumes its adult complexity and the swimming-plates appear. A thickening of the ectoderm on each side of the body gives rise to the epithelium of the tentacle and of its pouch. There are muscle-fibres forming the axis of the tentacle (*I, m,f.*). The calcareous bodies of the sense-organ are formed in the ectoderm cells of the apical pole, but gradually make their way on to the free surface of the cells, and become supported on four groups of fused cilia. Four outer groups of cilia unite with one another to form the bell (*s. o.*).

The most noteworthy points in this somewhat complex process of development are the following :—

1. The distinction between a purely protoplasmic part of the egg and a yolk-containing portion. In the Hydrozoa and Actinozoa the yolk-material is small in amount and evenly distributed, the egg being described as *alecithal* or *microlecithal*. In the present instance the yolk is at first accumulated in the centre of the egg, which is thus *centrolecithal* or mid-yolked, but soon the protoplasm accumulates at one end and the yolk at the opposite end of the developing embryo, producing a *telolecithal* or end-yolked condition.

2. The fact that cleavage is *unequal,* there being a distinction into large cells or macromeres, containing yolk, and purely protoplasmic small cells or micromeres.

3. The formation of a peculiar type of gastrula by epiboly or overgrowth, the ectoderm cells (micromeres) growing over and partly enclosing the endoderm cells (macromeres).

2. Distinctive Characters and Classification.

The Ctenophora are pelagic Cœlenterata in which the formation of colonies is entirely unknown. No indication of a polype-stage, so characteristic of the remaining Cœlenterata, can be detected either in the adult or in the embryonic condition. Ciliary movement, instead of being a merely embryonic form of locomotion as in the preceding classes, is retained throughout life, the cilia being fused to form comb-like structures, which are arranged in eight meridional rows or swimming-plates (costæ). Tentacles, when present, are usually two in number, situated in opposite (right and left) per-radii, and retractile into pouches. The enteron communicates with the exterior by a large stomodæum which functions as the chief digestive cavity. From the enteron is given off a system of canals, the ultimate branches of which are adradial and have a meridional position, lying beneath the swimming-plates; a single axial canal is continued to the aboral pole, where it commonly opens by two excretory pores. There are no gastric filaments. On the aboral pole, there is a single sense organ, having the character of a peculiarly modified lithocyst. The gonads of both sexes are lodged in the same individual, the ovaries and testes being formed on opposite sides of the meridional canals. The fertilized egg undergoes unequal cleavage, and the gastrula is formed by epiboly or overgrowth. There is no alternation of generations. In some cases development is accompanied by a well-marked metamorphosis.

The Ctenophora are divisible as follows :—

Sub-Class I.—Tentaculata (Micropharyngea).

Ctenophora possessing tentacles.

Order 1.—Cydippidea.

Tentaculata having two tentacles, retractile into sheaths, and unbranched meridional and stomodæal vessels. The body is either circular in section or is slightly compressed in the lateral plane.

Examples: *Hormiphora* (Fig. 161), and others (Fig. 168).

Order 2.—Cestidea.

Tentaculata having a band-like form, owing to the extreme compression of the body in the sagittal plane. The bases of the two principal tentacles are present, enclosed in sheaths, and there are also numerous lateral tentacles

contained in a groove. Union or anastomosis of the meridional and stomodæal vessels takes place.

Example: *Cestus* (Fig. 169).

ORDER 3.—LOBATA.

Tentaculata having numerous non-retractile lateral tentacles contained in a groove: the bases of the two principal tentacles are also present, but have no sheaths. The stomodæal and meridional vessels unite with one another. The body is compressed in the lateral plane, and is produced into two large oral lobes or lappets and into four pointed processes ora uricles.

Example: *Deiopea* (Fig. 170).

ORDER 4.—CTENOPLANIDEA.

Flattened Tentaculata of creeping or sessile habit, with a pair of retractile lateral tentacles. The costæ (swimming-plates), when present, are short and deeply sunk. There are no meridional canals; but there is a system of branching peripheral vessels.

Examples: *Ctenoplana* (Fig. 171), *Tjalfiella* (Fig. 172).

Sub-Class II.—Nuda (Macropharyngea).

Ctenophora without tentacles.

ORDER I.—BEROÏDEA.

Nuda in which the mouth is very wide, and the gullet occupies the greater part of the interior of the body. The meridional vessels are produced into a complex system of anastomosing branches.

Example: *Beroë* (Fig. 173).

3. GENERAL ORGANIZATION.

Compared with the two former classes of Cœlenterates, the Hydrozoa and Actinozoa, the organization of the Ctenophora, if we leave out of account the Ctenoplanidea, is remarkably uniform. This is due to the fact that nearly all the species are pelagic, none are colonial, and none form skeletons. Nevertheless a very great diversity of form is produced in virtue of differences in proportions and of modifications of the tentacular and canal systems.

The *Cydippidea* agree in all essential respects with Hormiphora, the most important deviation from the type-form being the compression of the body in the lateral plane in some genera, *e.g.*, *Euchlora* (Fig. 168, *2*), the result being an oval instead of a circular transverse section, with the tentacles at the end of the long axis. The aboral pole may be produced into wing-like appendages, as in *Callianira* (*1*), and in *Eulampetia* (*3*) the mouth is so dilatable as to form, when expanded, a sole-like plate by which the animal retains itself on the surface of the water or creeps over submarine objects. *Gastrodes parasiticum* is the only endo-parasitic Ctenophore known. Its larva, which resembles a

planula is found in the Tunicate Salpa. It is possible, however, that Gastrodes parasiticum is nothing but the larval stage of the free-living *Eulampetia pancerina.*

The *Cestidea* are represented by the remarkable " Venus's Girdle " (*Cestus veneris*), a band-shaped Ctenophore (Fig. 169) which sometimes attains a length of $1\frac{1}{2}$ metres, or nearly five feet. The body is greatly elongated horizontally in the sagittal, and compressed in

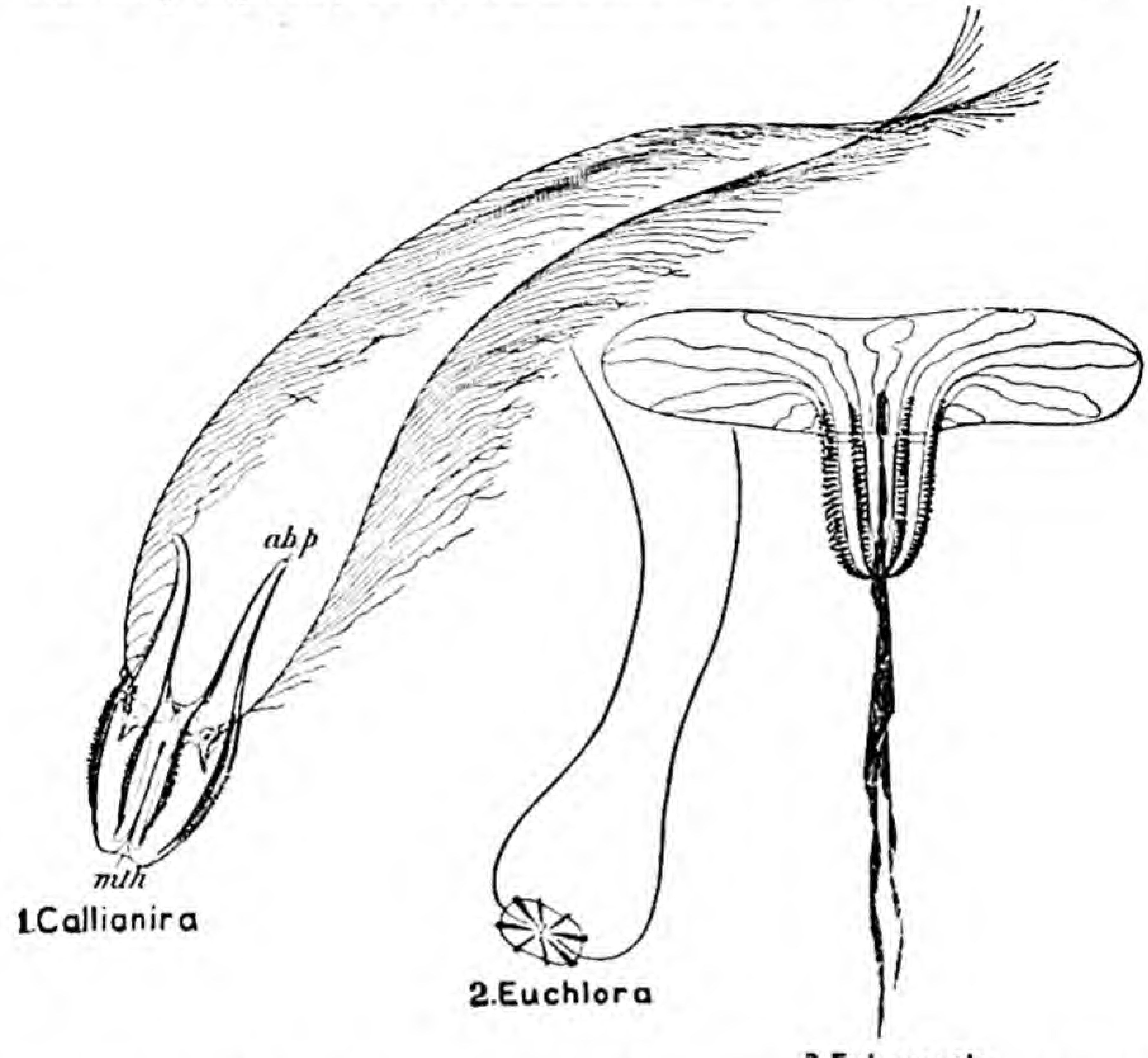


FIG. 168.—Three **Cydippidea.** *ab. p.* aboral process; *mth.* mouth. (After Chun.)

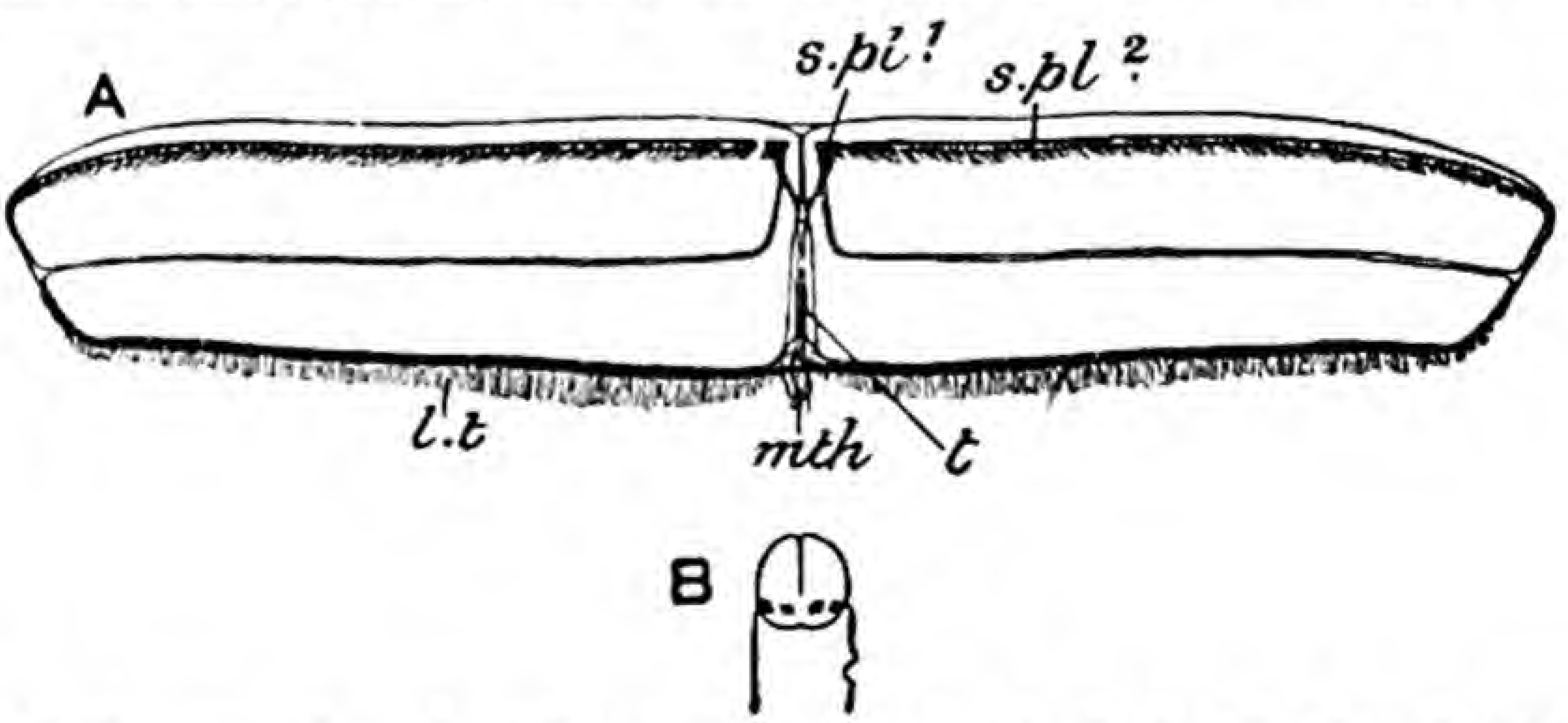


FIG. 169.—**Cestus veneris.** *A*, adult; *B*, young. *l. t.* lateral tentacles; *mth.* mouth $s.pl^1$., $s.pl^2$., swimming-plates; *t. tentacle.* (After Chun.)

the lateral plane, so as to have the form of a ribbon, which progresses by undulations of the whole body as well as by the action of its swimming-plates. Four of the swimming-plates (*s.* pl^1.) are very small; the other four (*s.* pl^2.) are continued all along the aboral edge of the body. The bases of the two principal tentacles (*t.*) are large and are enclosed in sheaths, and numerous small lateral tentacles (*l. t.*) spring from grooves which, in the present case, are continued the whole length of the oral edge. The young of Cestus (*B*) resembles a compressed Cydippid which undergoes gradual elongation in the median plane.

The *Lobata*, for instance *Deiopea*, are distinguished, as their name implies, by the presence of a pair of large lappets (Fig. 170, *A*, *lp.*), into which the oral surface is produced at either end of the sagittal plane. Four of the swimming-plates are shorter than the others, and at their bases arise elongated processes called *auricles* (*aur.*), which bear swimming-plates. The meridional canals communicate with the stomodæal canals, and from the connecting vessels curiously coiled vessels (*mrd. c.*) are given off into the lappets. The principal tentacles are usually absent in the adult, but are represented by their basal portions, which are small, situated at the oral end, and devoid of sheaths. From each tentacle-base grooves are continued along the oral surface to the auricles, and from the grooves depend numerous small lateral tentacles (*l. t.*). In the young condition the Lobata

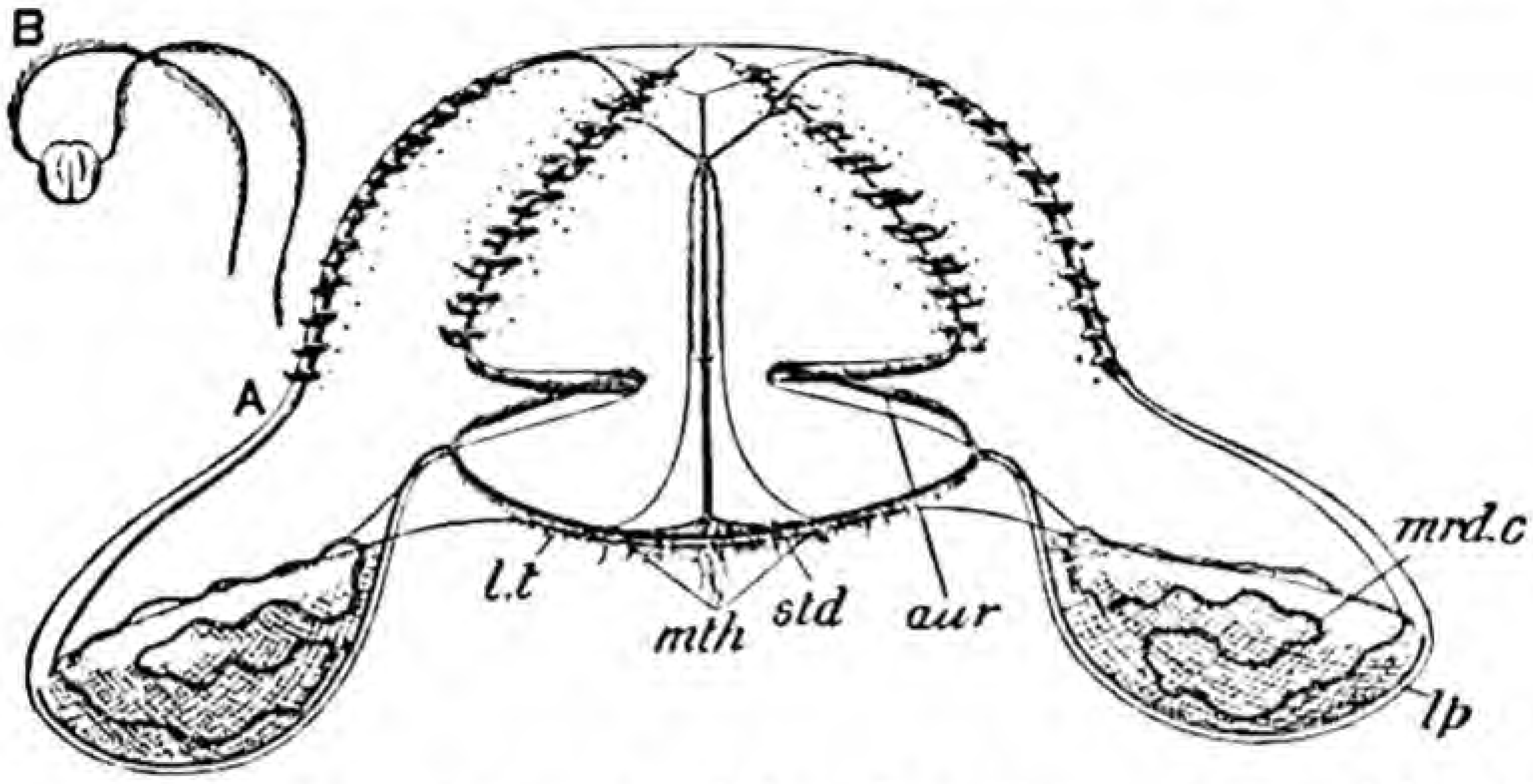


FIG. 170.—**Deiopea kaloknenota.** *A*, adult; *B*, young. *aur.* auricle; *lp.* lappet; *l. t.* lateral tentacles; *mrd. c.* meridional canal; *mth.* mouth. (After Chun.)

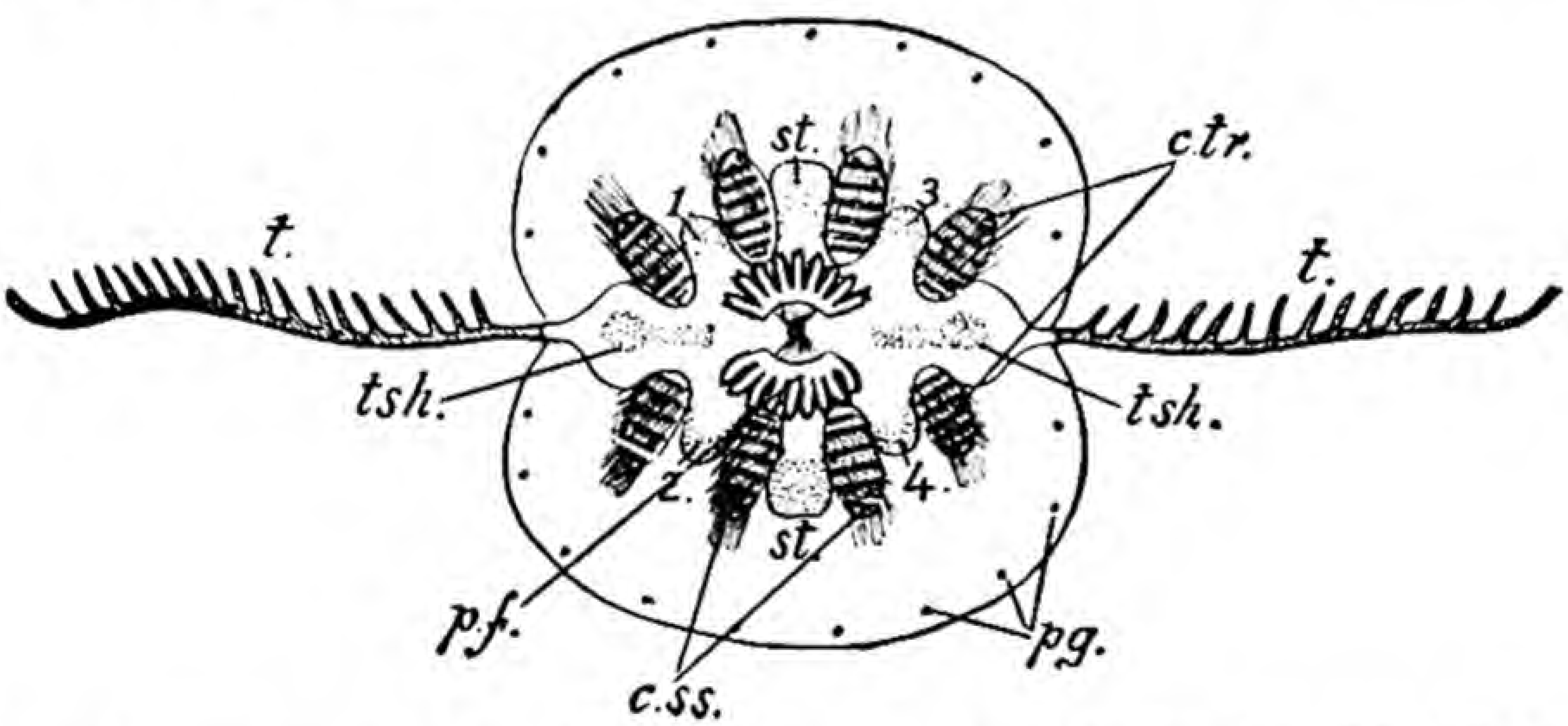


FIG. 171.—**Ctenoplana kowalevskii,** dorsal aspect. *t.* tentacles; *tsh.* tentacle sheaths; *ctr.* subtransverse costæ; *css.* sub-sagittal costæ; *st.* "stomach" (? stomodæum), *1, 2, 3, 4*, the four principal lobes of the infundibulum; *pf.* sensory tentacles representing the polar plates; *pg.* pigment spots. (After Willey.)

resemble such compressed Cydippidea as Euchlora, having a pair of long principal tentacles, no lappets, and unbranched vessels (*B*).

The *Ctenoplanidea* are represented by three genera—*Ctenoplana*, *Cœloplana*, and *Tjalfiella*.

Ctenoplana (Fig. 171) is a small marine animal, nearly circular in outline, flattened dorso-ventrally, and about 6 mm. in diameter. It has hitherto been found only twice—once off the west coast of Sumatra and once among the islands to the east of Papua. While able to swim freely, it is able also to creep on its ciliated oral or ventral surface. When it is swimming the animal draws downwards the edges of the disc so that it becomes somewhat helmet-shaped when viewed laterally. The organs of locomotion are eight small, deeply sunk swimming plates. In the centre of the aboral or dorsal surface is a polar body or sense-organ with a statolith, surrounded by a ring of small ciliated tentacles which are disposed bilaterally with reference to the transverse plane, but without polar plates (ciliated areas). The mouth is in the centre of the ventral (oral) surface. There

are two pinnate retractile tentacles. The canal-system is devoid of meridional canals, but comprises a set of branching and anastomosing peripheral canals. The male gonads only have been found: they are situated in diverticula of the canal system and have been described as having independent ducts opening on the exterior.

Cœloplana has been found in the Red Sea and on the coast of Japan. It is also flattened dorso-ventrally, and further resembles *Ctenoplana* in its ventral mouth, dorsal polar sense-organ, paired retractile tentacles, and anastomosing canals. There are, however, no swimming-plates, and progression is effected only by creeping.

Nothing is known of the development of either of these two genera.

Tjalfiella (Fig. 172) was found in dredgings from a depth of 500 metres off West Greenland. Instead of being free and pelagic like the Ctenophora in general, or able to creep about like *Cœloplana* and *Ctenoplana*, *Tjalfiella* is sessile in the adult condition, living attached to the stalk or polypes of an Umbellula (Pennatularia, p. 184). The body is elongated in the transverse plane: shortened in the direction of the primary

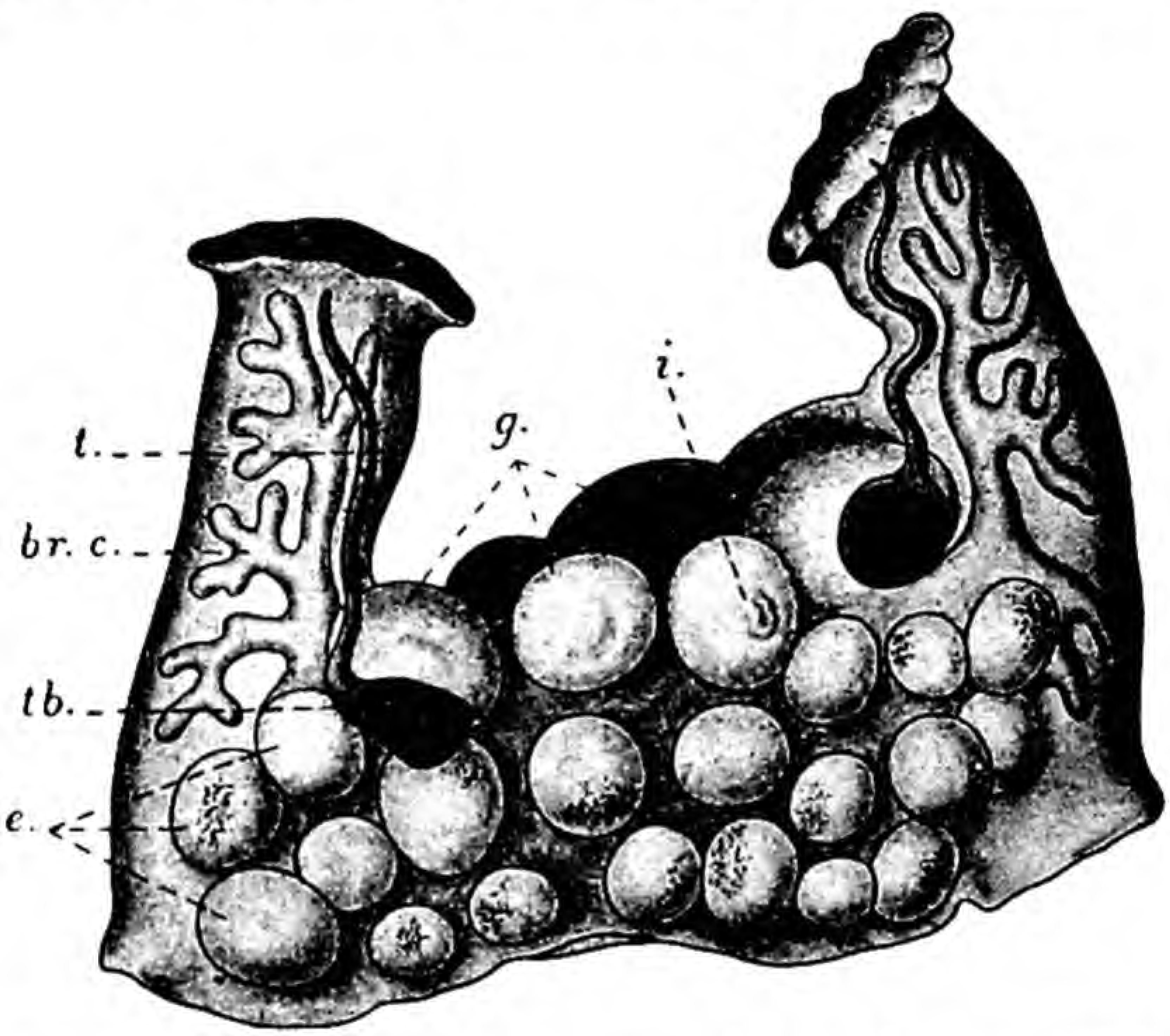


FIG. 172.—**Tjalfiella.** Adult specimen with many embryos, side view; oral (attached) surface upwards. *br. c.* branching canals; *e.*, *g.*, *i.* embryos; *t.* tentacle; *t. b.* tentacle base. (After Mortensen.)

axis. The attachment is effected by the oral surface by the agency of the inner surfaces of a pair of chimney-like hollow processes, each with a wide distal opening and a ciliated cavity. From the distal opening of each of these processes the corresponding retractile tentacle (*t.*) is capable of being protruded. The slit-like mouth, elongated, as in other Ctenophora, in the sagittal plane, opens out of a superficial sub-oral cavity with folded walls with which the cavities of the chimney-like processes are in free communication at their bases—the latter acting as secondary mouths. There are no meridional or stomodæal canals, and in the adult no swimming-plates: the polar (apical) sense-organ is reduced. There are four pairs of reproductive organs, each comprising an ovary and testis arranged opposite one another as in Hormiphora and the Ctenophora in general, but, in the absence of meridional canals, situated in rounded outgrowths of the per-radial or transverse canal. The inter-radial canals give off lateral branching, but not anastomosing, canals.

Tjalfiella differs from all the rest of the Ctenophora in being viviparous. The young, escaping by rupture of the body-wall of the parent from the brood-pouches (apparently in the canal-system) in which they are developed, are provided each with eight swimming-

plates and pursue a free existence for a time, subsequently becoming attached and losing the swimming-plates.

[*Bathyctena*, also a deep-sea form, with some resemblances to Tjalfiella, is more nearly related to the normal Cydippidea.]

The Ctenoplanidea are of greatest interest owing to the possibility of their representing an intermediate stage between Cœlenterates (through ordinary Ctenophores) and Platyhelminthes (see Section V).

Beroë, the principal genus of the *Beroïdea*, has the form of a cylinder (Fig. 173), one end of which is rounded and bears the sense-organ, the other truncated and occupied entirely by the immense mouth (*mth.*). The greater part of the body is taken up by the huge stomodæum; the infundibulum (*inf.*), per-radial and infundibular canals, etc., all being crowded into a small space at the aboral pole. The meridional canals send off branches which unite with one another, forming a complex network of tubes, and at their oral ends the four meridional canals of each (right and left) side and the corresponding stomodæal canal unite into a horizontal tube, which runs parallel with the margin of the mouth. There is no trace of tentacles either in the adult or in the embryonic condition. It is for this reason and because of the enormous development of the stomodæum that the Beroïdea are separated from the rest of the Ctenophora, as the only order of the sub-class Nuda (Macropharyngea).

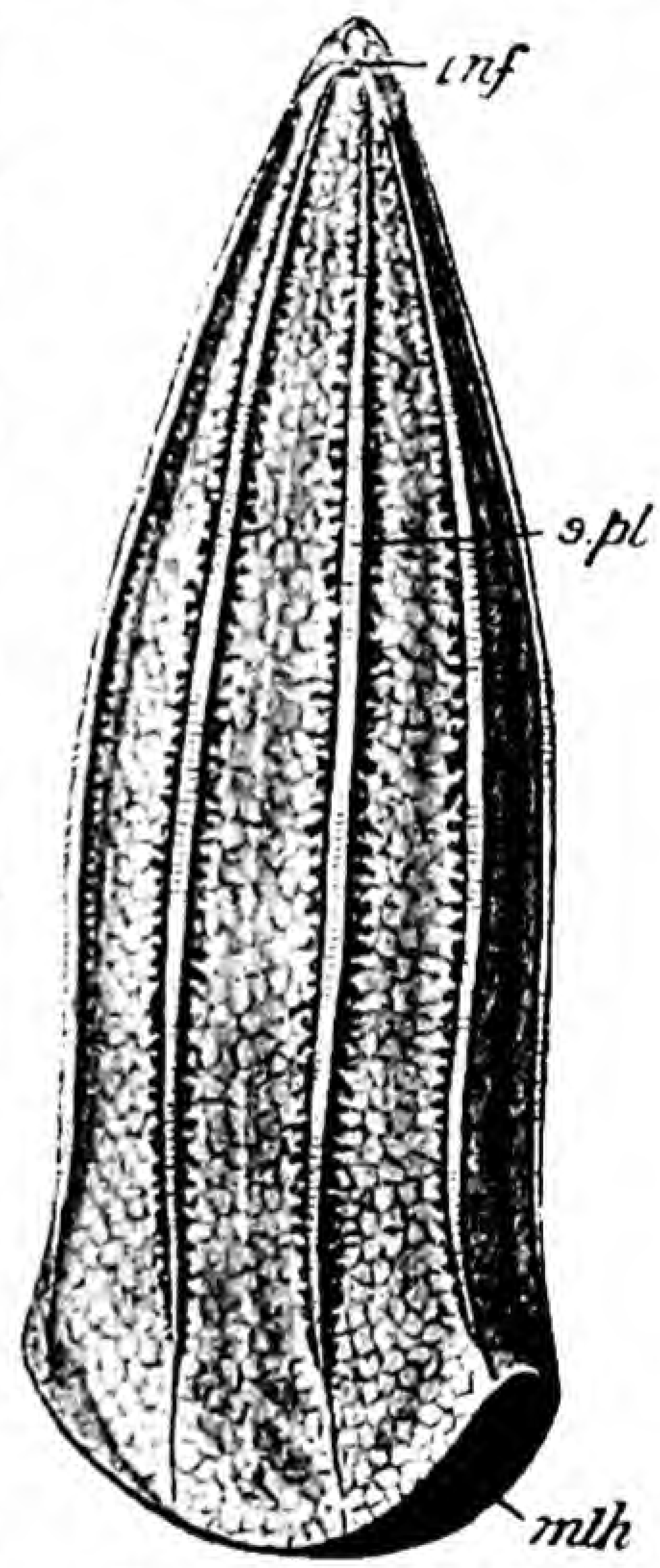


FIG. 173.—**Beroë forskalii.** *inf.* infundibulum; *mth.* mouth; *s. pl.* swimming-plates. (After Chun.)

The Ctenophora are usually perfectly transparent, and quite colourless, save for delicate tints of red, brown, or yellow in the tentacles and stomodæal ridges. Cestus has, however, a delicate violet hue, and when irritated shows a beautiful blue or bluish-green fluorescence. Beroë is coloured rose-pink.

Ctenophora are found in all seas from the arctic regions to the tropics. As is to be expected from their perishable nature, there is no trace of the group in the fossil state.

Bolinopsis vitrea, one of the Lobata, a Ctenophore which attains a diameter of 25–40 mm., while still in the larval or cydippid condition and not more than 0·5–2 mm. in diameter, becomes sexually mature, the gonads producing ripe ova and sperms; and the eggs are fertilized and develop in the usual manner. Soon the gonads degenerate, the larva metamorphoses into the adult form, and a second period of sexual maturity supervenes. This precocious ripening of sex-cells probably occurs in many Ctenophora.

THE RELATIONSHIPS OF THE CŒLENTERATA.

There can be little doubt that the lowest cœlenterate form known to us is the simple hydrozoan polype, represented by Hydra and by the hydrula stage of many Hydrozoa. Somewhat more complex in virtue of its gastric ridges and filaments is the scyphozoan polype, represented by the scyphistoma of Aurelia. Still more complex is the actinozoan polype, or *actinula*, as it may be

called with its large stomodæum, mesenteries and mesenteric filaments, and elaborate muscular system. Speaking generally, one may say that these three polype-forms represent as many grades of organization along a single line of descent.

The medusa-form in the Hydrozoa is, as we have seen, readily derived from the hydrula by the widening out of the tentacular region into an umbrella. We may thus conceive of the Trachylinæ, or hydroid medusæ with no fixed zoophyte stage, as being derived from a pelagic hydrula.

The Hydroidea may be considered to have arisen in consequence of the adoption of asexual multiplication, by budding, during the larval or hydrula stage. Instead of the hydrula giving rise directly to a medusa, we may suppose it to have formed a temporary colony by budding, after the manner of the Hydra, the individual zooids being ultimately set free as medusæ. The next stage would be the establishment of a division of labour, in virtue of which a certain proportion only of the zooids became medusæ, the rest retaining the polype-form, remaining permanently attached, and serving for the nourishment of the asexual colony.

The Hydrocorallina appear to be a special development of the hydroid stock, the nearest affinities of the order being with such forms as Hydractinia.

The Siphonophora may be conceived as having originated from a hydrula specially modified for pelagic life by the conversion of the basic disc into a float—something after the fashion of Minyas (Fig. 155). In such a form extensive budding, accompanied by division of labour, would give rise to the complex siphonophoran colony.

The most primitive Scyphozoa are the Lucernaridæ. They combine polype-like with medusoid characters, and appear to have branched off the line of descent early in the phylogenetic development of the Scyphozoa. The Cubomedusæ, Semæostomeæ, and Rhizostomeæ may be said to represent three grades of increasing complexity along the general line of descent, the Coronata diverging somewhat. It is to be noted, however, that such a supposed line does not lead towards the simpler Actinozoa, but towards a type diverging from the latter as well as from the Lucernaridæ, Cubomedusæ, and part of the Coronata—in as far as septa or mesenteries are absent in the adult condition.

The close similarity of Edwardsia and the Octocorallia in the number and arrangement of the mesenteries seems to indicate the derivation of both Hexacorallia and Octocorallia from a common ancestor in the form of a simple actinozoan polype or actinula. Edwardsia clearly leads us to the Actiniaria or typical Sea-anemones, and the Madreporaria are undoubtedly to be looked upon as skeleton-forming Actiniaria.

The relationships of the Ctenophora to the cnidarian Cœlenterates are very doubtful. An attempt was even made to demonstrate that their relationship

to the Porifera is closer than that to any of the Cnidaria. However, Ctenaria, one of the Anthomedusæ (Fig. 113, *1*), presents some remarkable resemblances to a Cydippid, such as Hormiphora. It has two tentacles, situated in opposite per-radii, and each having at its base a deep pouch in the umbrella, resembling the sheath of Hormiphora. There are eight radial canals formed by the bifurcation of four inter-radial offshoots of the stomach, and corresponding with them are eight bands of nematocysts diverging from the apex of the ex-umbrella. If these striking resemblances indicate true homologies, we must compare the whole sub-umbrellar cavity of Ctenaria with the stomodæum of Hormiphora, the margin of the bell of Ctenaria with the mouth of Hormiphora, and the mouth of Ctenaria with the aperture between the stomodæum and the infundibulum of Hormiphora. But, as we have seen, the gullet of Ctenophora is a true stomodæum developed as an in-pushing of the oral ectoderm, and has therefore a totally different origin from the sub-umbrella of a medusa. Moreover, the tentacles of Ctenaria have no muscular base contained in the sheath, but spring from the margin of the umbrella as in other Hydrozoa: its gonads are developed in the manubrium, not in the radial canals, and there is no trace of an aboral sense-organ.

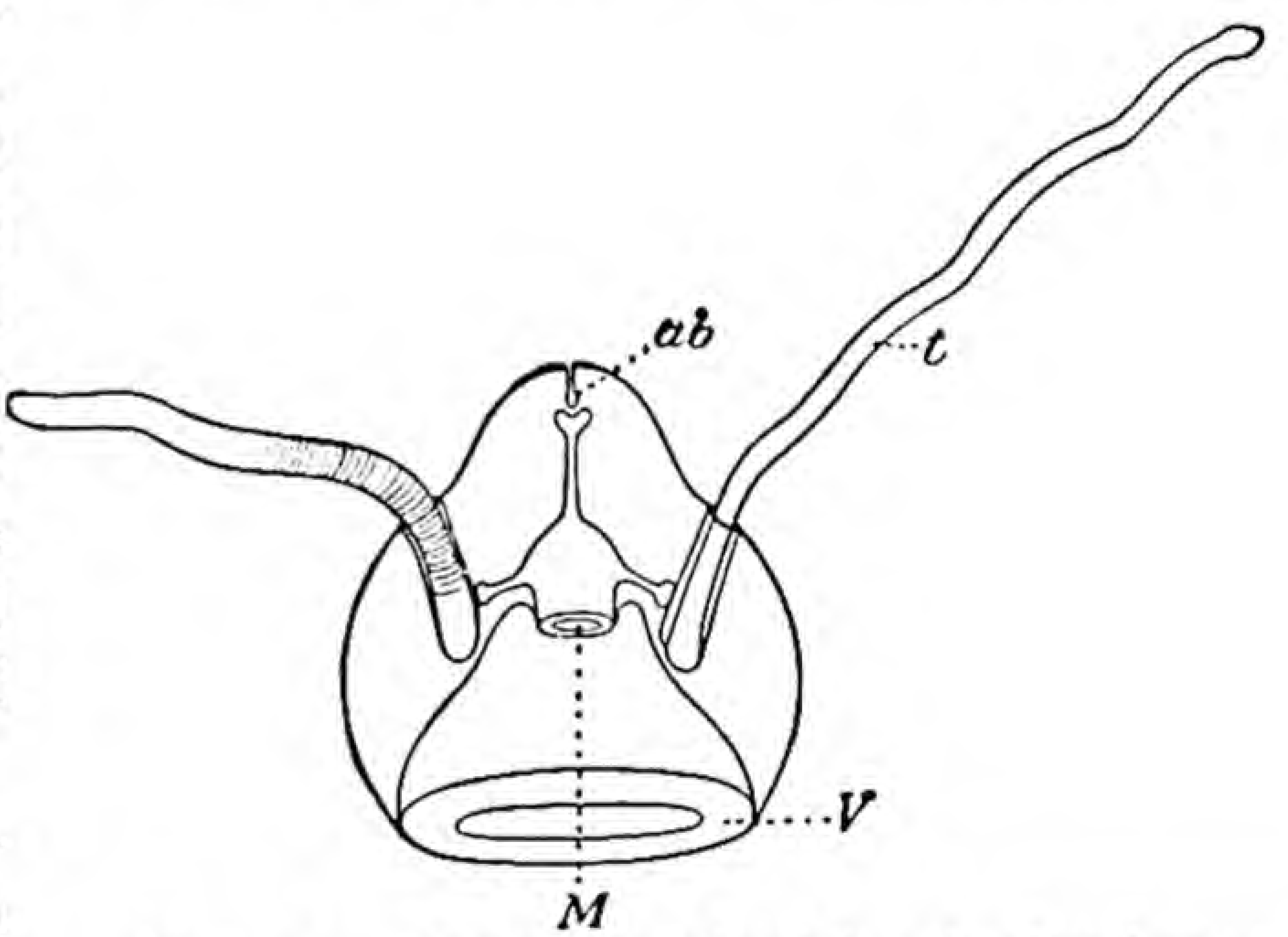


FIG. 174.—**Hydroctena salenskii.** *ab.* aboral sense-organ; *M.* manubrium; *t.* tentacle; *V.* velum. (From the *Cambridge Natural History*, after Dawydoff.)

In the case of the Narcomedusa *Hydroctena*, found in Malayan seas, the ctenophoran resemblances, if only superficial, are much more striking. *Hydroctena* (Fig. 174) is bell-like, and provided with a velum (*V*). At its apex is an ampulla (*ab.*) bearing two calcareous bodies supported on spring-like processes of the epithelium. From the apex of the gastric cavity a canal is given off which extends to the sense-organ, where it ends blindly, and from the sides a pair of short canals, each of which terminates blindly at the base of the corresponding tentacular sheath. Only two tentacles are present, with sheaths at their bases: these are situated, not on the margin of the bell, as in a medusa, but between it and the apex. There are no traces of swimming-plates, and, so far as the evidence at present forthcoming goes, there is no sufficient evidence to establish ctenophoran affinities.

On the other hand, the resemblance between transverse sections of an embryo Ctenophore (Fig. 175, *B*) and of an embryo Actinian (*A*) is very striking, and the presence of a well-developed stomodæum, and of gonads developed in

connection with the endoderm and discharging their products through the mouth, may be taken as further evidences of affinity between the Ctenophora and the Actinozoa.

The special characteristics of the Ctenophora are, however, so numerous and so striking, and their development is so utterly unlike that of any of the other Cœlenterata, that in our present state of knowledge it is impossible to determine their affinity with the other classes with any degree of certainty. In regard to the phylogenetic history of the Metazoa the various resemblances between the Ctenophora and the turbellarian type of the Platyhelminthes are of considerable importance. As pointed out before, the Ctenoplanidea may well represent an intermediate stage between the Cœlenterates and the Platyhelminthes.

As to the orders of the Ctenophora, it seems tolerably clear that both Cestidea and Lobata are derived from cydippid forms, since they both pass through, in the course of development, a stage closely resembling the lower Cydippidea. The Beroïdea are more highly organized in certain respects, *e.g.*, in the details

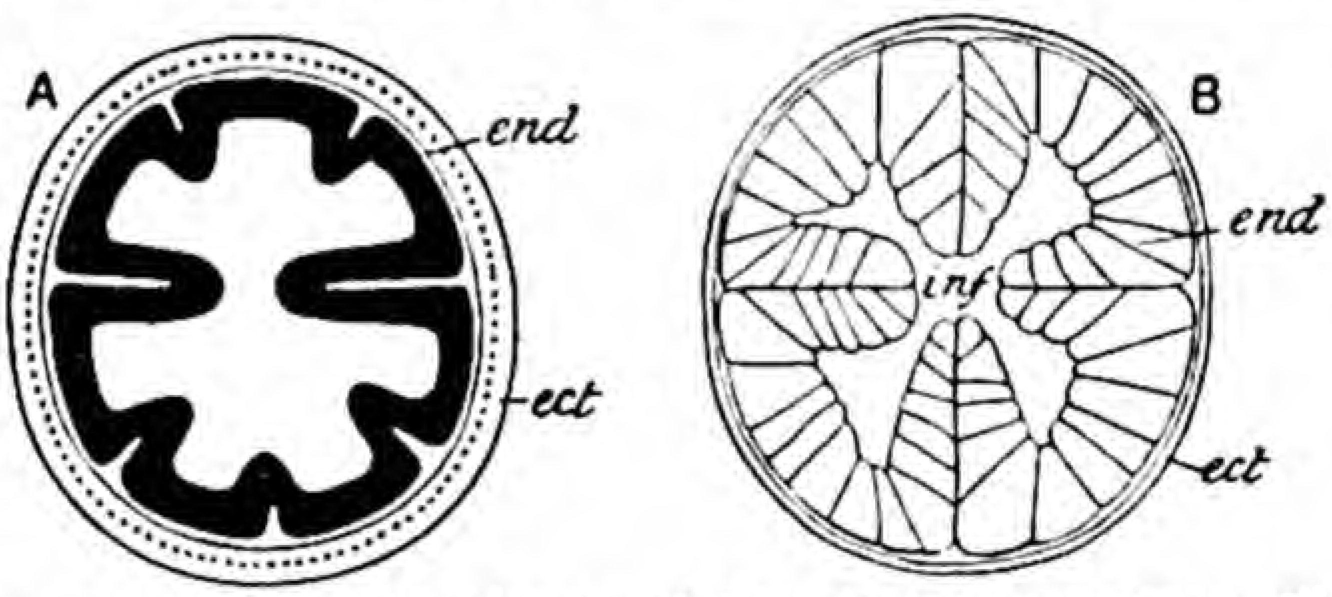


FIG. 175.—Transverse section of embryos of **Actinia** (*A*) and **Beroë** (*B*). *ect.* ectoderm; *end.* endoderm; *inf.* infundibulum. (After Chun.)

of their histology, than the other Ctenophora, and it seems quite possible that they may be derived from tentaculate forms. Whether the Ctenoplanidea are primitive or specially modified remains doubtful; but the latter, in view of the larval development of *Tjalfiella*, appears the more probable conclusion.

By many others the Sponges have been looked upon as so closely related to the Cœlenterata that they may be regarded as members of the same great phylum. The points of resemblance are readily to be recognized: the simple structure, with the large central cavity into which a wide opening—the mouth or the osculum, as the case may be—leads; the absence of a well-developed mesoderm, the fixed mode of life, and associated with it the tendency to form compound structures by a process of budding. In addition, the occurrence of larval stages which have at least a superficial correspondence in the two phyla, would appear to constitute an important connecting link. But a closer examination of the subject shows that some of these apparent points of resemblance are superficial only, and establishes a number of differences between Sponges and Cœlenterates too important to allow us to suppose that a close relationship

exists. One of these differences stands out beyond the others as the most radical. The osculum of a sponge is found, when we trace the development of the larva, to correspond in no sense with the mouth of the Cœlenterate. This alone, apart from important differences in the adult structure, such as the presence in the wall of the Sponge of the system of inhalant apertures, the presence of the peculiar collared gastric cells, and the absence of stinging-capsules, would suffice to remove the Sponges from the Cœlenterata, and place them in a phylum apart. But not only is the grouping of Sponges and Cœlenterates in one phylum thus rendered impossible by important differences in their structure and development; a comparison of the mode of formation of the embryonic layers in the two groups shows such radical dissimilarity that it is scarcely possible to find sufficient evidence for regarding them as having been derived from the same metazoan ancestors, and there is much to be said in favour of the view that they have originated separately from the Protozoa. It is for this reason that the Sponges are included in a separate sub-kingdom, viz., the Parazoa.

APPENDIX TO THE CŒLENTERATA.

THE MESOZOA.

Under the designation MESOZOA have been comprised certain lowly organized animal forms, formerly supposed to afford us something of the nature of a connecting link between the Protozoa and the Metazoa, but now more generally looked upon as degenerate members of the latter subdivision. It has been proposed to term them the *Moruloidea*, from the resemblance which they bear to the morula stage in embryonic development.

They are all multicellular. Their integument is formed by one layer of ciliated cells representing a so-called *somatoderm*. A true endoderm and a mesoglea are absent, the somatoderm covering a single axial cell from which reproductive cells are formed. The Mesozoa comprise at least three families, the *Dicyemidæ*, the *Heterocyemidæ*, and the *Orthonectidæ*, all the members of which are internal parasites.

The *Dicyemidæ* are parasites in the kidneys of various Cuttle-fishes and Octopods (*Cephalopoda*). Dicyemennea (Fig. 176), the length of which is between 0·75 and 6 or 7 millimetres, consists of a head-part or *calotte*, and an elongated body. The form of the calotte varies a good deal, according to age; in young specimens it is isotropic (*i.e.*, symmetrical around the long axis); in the adult condition ventral and dorsal sides are distinguishable. It consists of a swollen disc of four cells and a ring of four or five *pole cells*. The cells of the head all bear cilia, which are shorter and thicker than those of the body-cells.

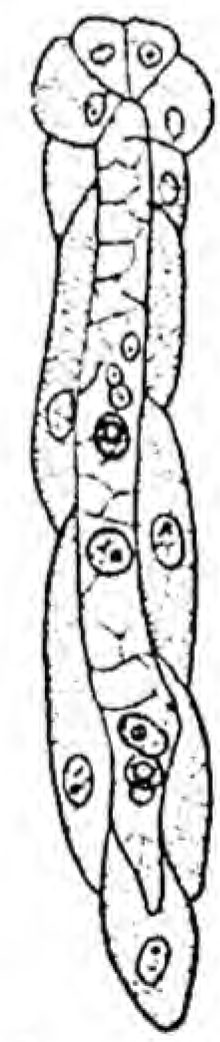


FIG. 176.—**Dicyemennea gracile,** young individual. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Hartmann.)

The body consists of a single large axial cell, and of a single layer of outer cells which completely invest the axial cell. The outer cells which follow immediately on the head are distinguishable from the rest by their granular contents, and by their being dilated internally in such a way that the apex of the axial cell is constricted.

The axial cell is either almost completely cylindrical or spindle-shaped, and is covered in its entire extent by the outer cells. It presents a differentiated cortical layer, beneath which the finely granular gelatinous contents are at first homogeneous, but afterwards become vacuolated. In the middle of the cell is a large oval or ellipsoidal nucleus.

The life-history is a true alternation of generations. The primitive nucleus of the axial cell divides mitotically to form a smaller asexual germ-nucleus and a larger nucleus —the definitive nucleus (somatic nucleus) of the axial cell. Further germ-nuclei result from subsequent divisions. The germ-cells undergo a process similar to cleavage. Of the cells thus formed one gives rise to the axial cell of the embryo: the others, increasing in numbers and becoming smaller, gradually grow over the axial cell until they at length completely enclose it. The embryo increases greatly in length, and escapes from the interior of the parent, which it completely resembles, by perforating the body-wall. This phase of the parent animal (Fig. 177) is the phase to which the term *nematogene* is applied: the asexually developed young are the so-called *vermiform embryos*. The latter swim about for a time in the fluid of the kidney of the host; afterwards they attach themselves by means of a head to certain appendages—the venous appendages—of the walls of the cavity. A number of generations of these asexually developed forms succeed one another until, when the venous appendages of the kidney have become thickly infested with the parasites, a change takes place, and a sexual process of multiplication is initiated. In the interior of the nematogene a change is observable, and female sexual individuals are formed instead of vermiform embryos. Unlike the latter the former do not leave the body of the parent; they also differ in the non-development of an enclosing layer, the cells representing the latter being converted into ova. In their development, as in that of the vermiform embryos, the nucleus of the axial cell of the female divides into two. One of these becomes the permanent somatic nucleus of the axial cell: the other gives rise to the nucleus of the primitive ovum, and surrounds itself with protoplasm. This divides to give rise to a number of ova, which become more numerous till they come to fill the axial cell. Then the first generation of ova is discharged into the protoplasm of the parent axial cell: this first generation of ova is derived from the cells representing the outer layer. Later, further generations of ova, which are the descendants of the primitive ova, make their escape. These all eventually wander away into the protoplasm of the axial cell of the parent, increase in size, undergo a process of maturation, and become fertilized. Fertilization is effected by means of typical tailed sperms developed in a second set of sexual individuals, the males (Fig. 178), which were formerly known as the *infusoriform embryos*. In its mature form the male is approximately pear-shaped, the narrower end being posterior. Several axial cells are present: these form the *testes*, in which the sperms are developed. They are surrounded by the outer cells, which at the posterior end take the form of a flat ciliated epithelium. The complete development of the sperms only takes place when the young male leaves the host in which it was formed and seeks a new one; thus it is only by the sperms of a male from another host that the ova can be fertilized. Males are developed from the fertilized ova and subsequently escape, their development being similar to that of the vermiform embryos; the phase of the parent form to which they are developed is that known as the *rhombogene*. After a number of generations of males have been formed in this way, the rhombogene undergoes modification, and the last generation of fertilized ova gives rise, not to males, but to vermiform embryos—*i.e.*, to an asexual generation—and with these the cycle begins anew.

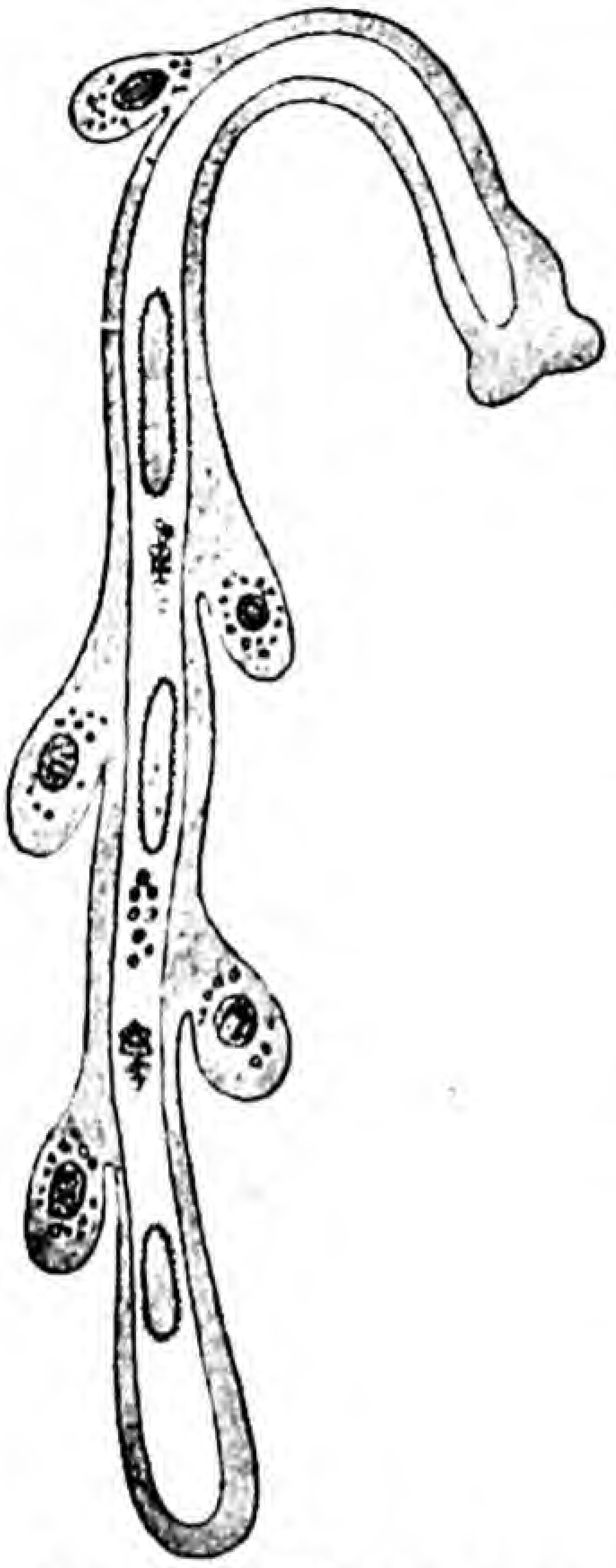


FIG. 177.—**Dicyema paradoxum,** with vermiform embryos. (From Bronn's *Tierreich*, after Kölliker.)

FIG. 178.—Male of **Dicyema paradoxum.** (From Bronn's *Tierreich*, after Kölliker.)

The *Heterocyemidæ*, which are also parasites of the Cephalopoda, resemble the Dicyemidæ in most respects, but the head is wanting.

The family *Orthonectidæ* comprises only two genera—*Rhopalura* and *Stœcharthrum*—

which live as parasites in a Polyclad (*Leptoplana*), a Nemertine (*Lineus*), an Annelid, and a Brittle-Star (*Amphiura*). In the stage that represents the asexual form of the Dicyemidæ the Orthonectid assumes the character of a plasmodium, or mass of finely granular protoplasm containing many nuclei, and is capable of active amœboid movements. In the interior of the plasmodia the sexual forms are developed. A nucleus of the plasmodium surrounds itself with protoplasm and gives rise to a germ-cell, which by a process of cleavage develops into the sexual stage. In some cases only males are developed in one plasmodium and females in another: in others both sexes are formed together in the same plasmodium. In some forms the sexes are united. The sexual animals, especially the females (Fig. 180), bear a considerable resemblance to the Dicyemidæ, but instead of the axial cell there are a number of cells, the ova or sperm-cells. The outer cells are arranged in segments or rings. In front is usually a region composed of a few rings in which the outer cells bear

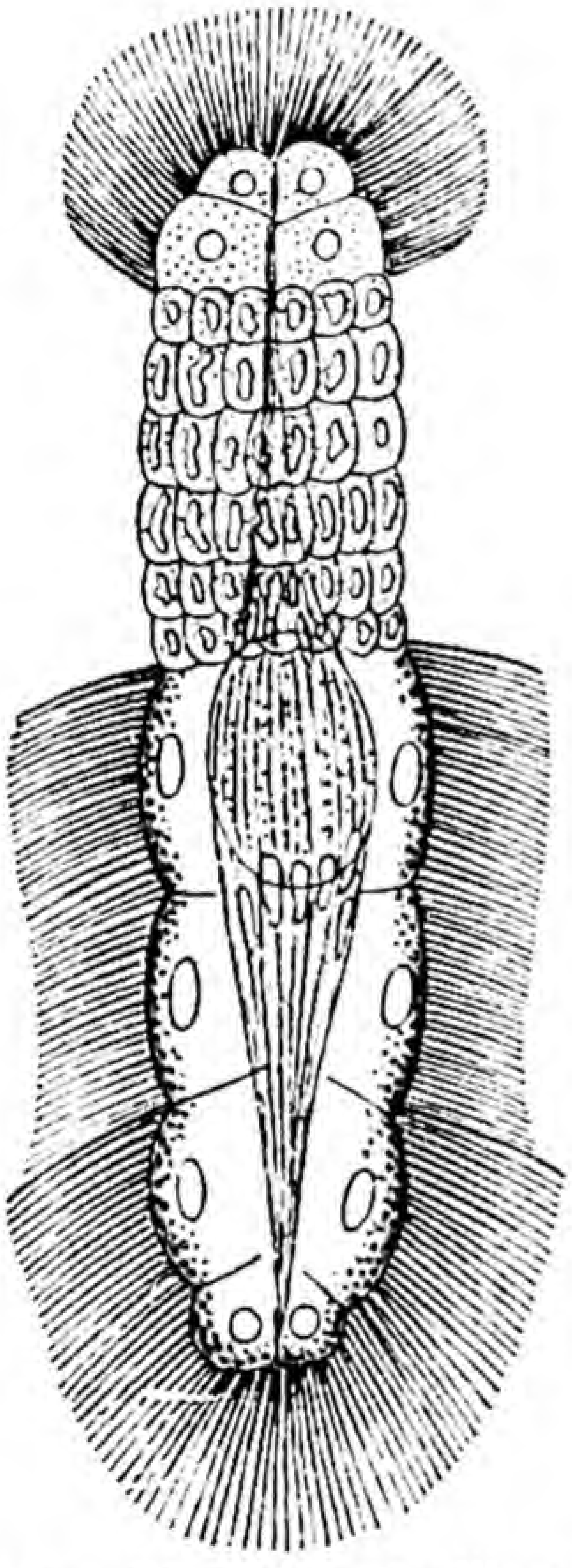


FIG. 179.—**Rhopalura giardii,** male. (From Bronn's *Tierreich*, after Julin.)

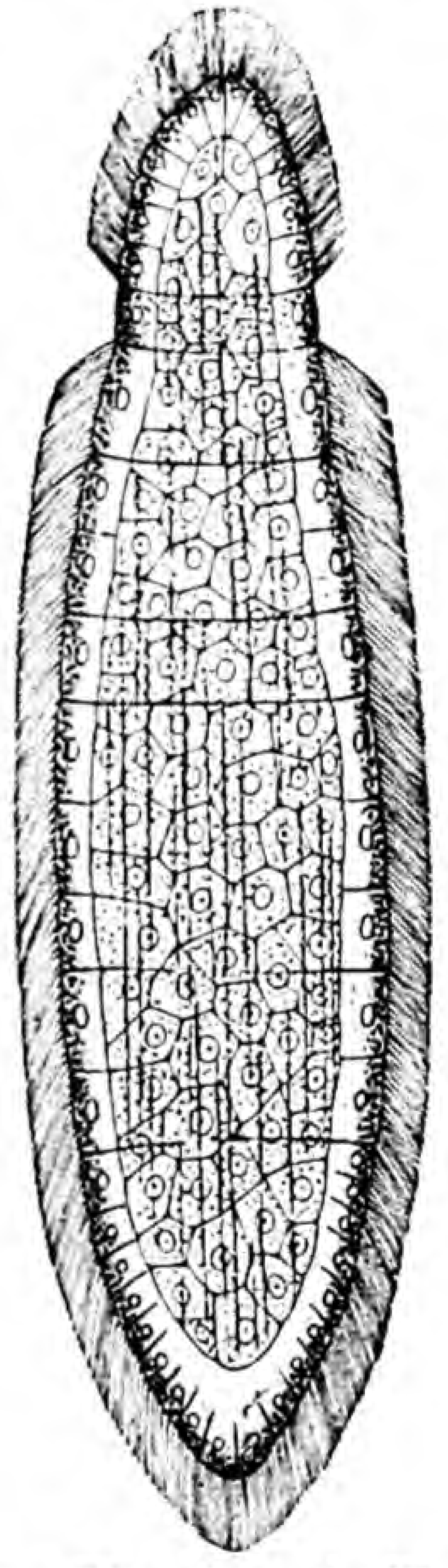


FIG. 180.—**Rhopalura giardii,** female. (From Bronn's *Tierreich*, after Julin.)

cilia which are directed forwards: then comes a shorter region devoid of cilia, and behind that is the longest region, having cilia directed backwards. In shape the body is usually spindle-like—the males (Fig. 179) differing somewhat from the females. In about the middle of the internal space of the male is the compact oval testis containing small tailed sperms. Beneath the outer layer in the male, but not in the female, is a layer of fibres sometimes regarded as muscular. The plasmodia multiply by fragmentation. The development of the embryos either goes on in the intact plasmodium, or the latter breaks up and the embryos are to be found at various stages free in the host.

In the development of a male from the germ-cell the first cleavage is unequal. The further cleavage results in the formation of a solid morula. The outer cells become differentiated into two distinct groups, the one giving rise to the external layer of the anterior region, the other to that of the posterior region of the body. The inner cells

multiply and give rise to the numerous small spermatocytes of the testis. The formation of the layer of the fibres only takes place later.

In the case of the female the cleavage appears to be equal from the first, and results in the formation of a blastula-like stage, which becomes converted into a solid morula-like body by the passing inwards of a number of cells. As in the male, the central cells multiply to form the sexual cells, and the outer cells form the external layer with its segments. In all probability, though this has not been actually proved, the mature sexual animals

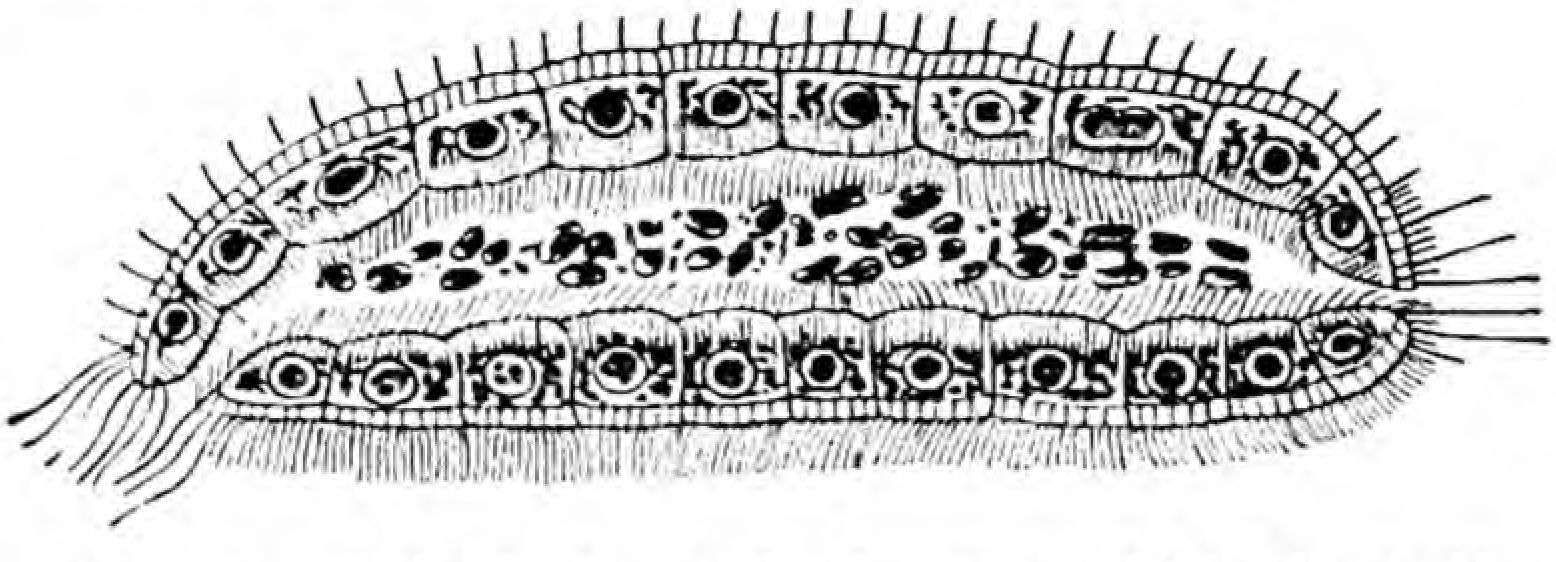


FIG. 181.—**Salinella,** longitudinal section. (After Frenzel.)

become free from the plasmodia, and the females, after fertilization, find their way to another host where they are transformed into plasmodia, the germ-cells of which are the fertilized ova.

To be mentioned also in connection with the Dicyemidæ and Orthonectidæ, as perhaps allied with them, are the remarkable parasites *Amœbophrya* and *Lohmanella*—the former living in certain Radiolarians (*Protozoa*), the latter in the body-cavity of a *Fritillaria* (*Urochorda*). These both resemble the groups described above, and differ from the other Metazoa, in the presence of only a single body-layer. This remarkable simplicity of body-structure occurs also in *Salinella*, though too little is known with regard to this animal to provide adequate data for determining its affinities with certainty.

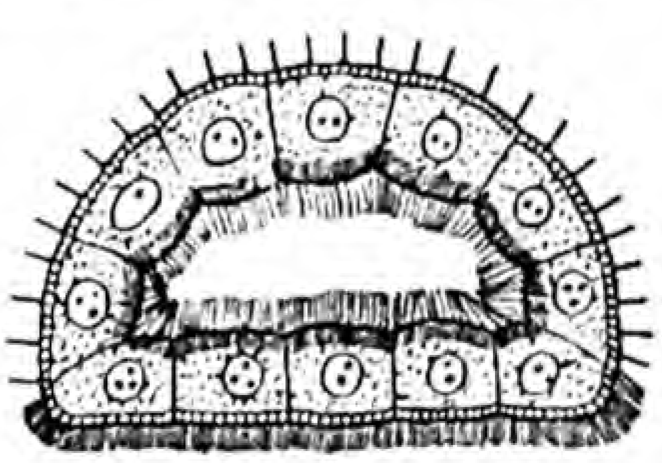


FIG. 182.—**Salinella,** transverse section. (After Frenzel.)

Salinella (Figs. 181 and 182), which has only been found in artificial saline solutions, is a minute animal in the form of a somewhat depressed cylinder, open at both ends, and with a wall composed of a single layer of cells. The anterior end is somewhat pointed; around the anterior opening or *mouth*, which is ventrally directed, is a circlet of from fifteen to twenty long whip-like cilia. The posterior aperture (*anus*), which is usually closed, is surrounded by a few stiff setæ. The ventral surface is flattened, and is covered with fine vibratile cilia, while on the dorsal surface and the sides are regularly arranged rows of straight " setæ " (non-motile cilia). The internal cavity (*enteron*) is found to contain sand, plant-fragments, and Bacteria; its surface is beset with long cilia. Multiplication is said to take place by transverse fission.

Trichoplax and *Treptoplax*, which have been supposed to be Mesozoa, appear to be merely special modifications of developmental phases of *Hydrozoa*.

SECTION V

PHYLUM PLATYHELMINTHES

The *Platyhelminthes* or Flat-Worms are a group of soft-bodied, bilateral, usually flattened animals, which are devoid of true metameric segmentation. With a sufficient degree of uniformity of structure to render the phylum a fairly compact and well-defined one, there is yet a considerable range in complexity, from the simplest forms—certain of which have been supposed to be nearly connected with the Ctenophora among the Cœlenterata—to the highest, which have all the various systems of organs very much more highly developed. The body is built up from three embryonic layers—*ectoderm*, *mesoderm*, and *endoderm*—as in all higher groups of animals. An excretory vascular system of a peculiar kind—the *water-vascular* or *protonephridial system*—is present in nearly all members of the phylum. A body-cavity (see following Sections) is not present, the spaces between the various organs and the wall of the body being filled up with a peculiar form of connective-tissue termed the *parenchyma*. The egg is in most instances composite, the egg-shell enclosing not only the fertilized ovum, but a quantity of nutrient material or *food-yolk*, derived, in most instances, from a special set of glands, the *yolk* or *vitelline glands*.

The main features which distinguish the Platyhelminthes from the Cœlenterata are the pronounced bilateral symmetry with the many secondary features which it involves, the presence of a middle embryonic layer or mesoderm, and the non-occurrence of fixed colonies formed by budding.

1. Examples of the Phylum.

i. A Fresh-water Triclad (*Planaria* or *Dendrocœlum*).[1]

General Features.—Species of fresh-water Planarians of the genera *Planaria* and *Dendrocœlum* are common in the mud at the bottom of ponds of fresh-water in all quarters of the globe. They are small, thin, flattened worms a few millimetres in length, broader at one end, the *anterior*, than at the other, the *posterior*, which is more or less pointed. The animal (Figs. 183, 184, 188) is very readily recognized to be *bilaterally symmetrical*, with an *upper* or *dorsal* and a *lower* or *ventral* surface, *right* and *left* borders, and *anterior* and *posterior* ends. The colour varies in different species and in different individuals, but is usually grey, red, brown, or black. Movements of locomotion in the direction

[1] The account is sufficiently general to apply to species of either of these genera.

of the long axis of the body are recognizable in the living animal. Sometimes this is a steady gliding movement, which is brought about by the action of a coating of vibratile cilia on the surface; sometimes the worm glides along by

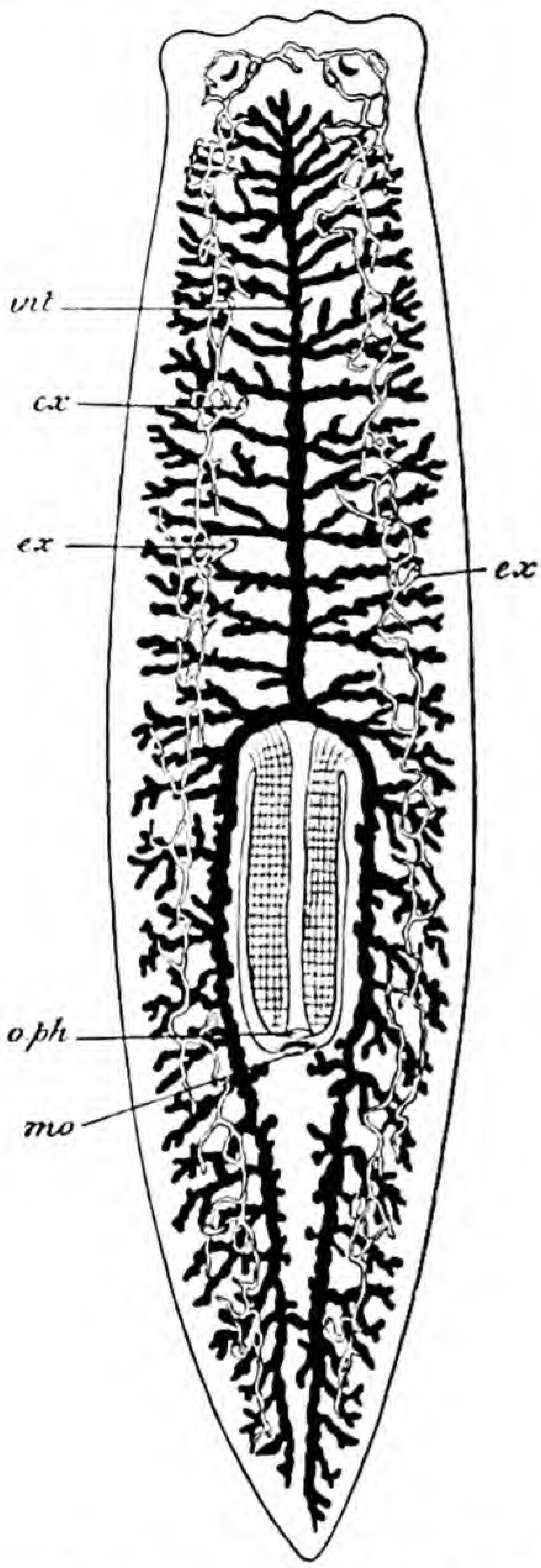


FIG. 183.—**Planaria.** Digestive and excretory systems. *ex.* openings of excretory system; *int.* intestine; *mo.* mouth; *o. ph.* opening of pharnyx. (After Jijima and Hatschek.)

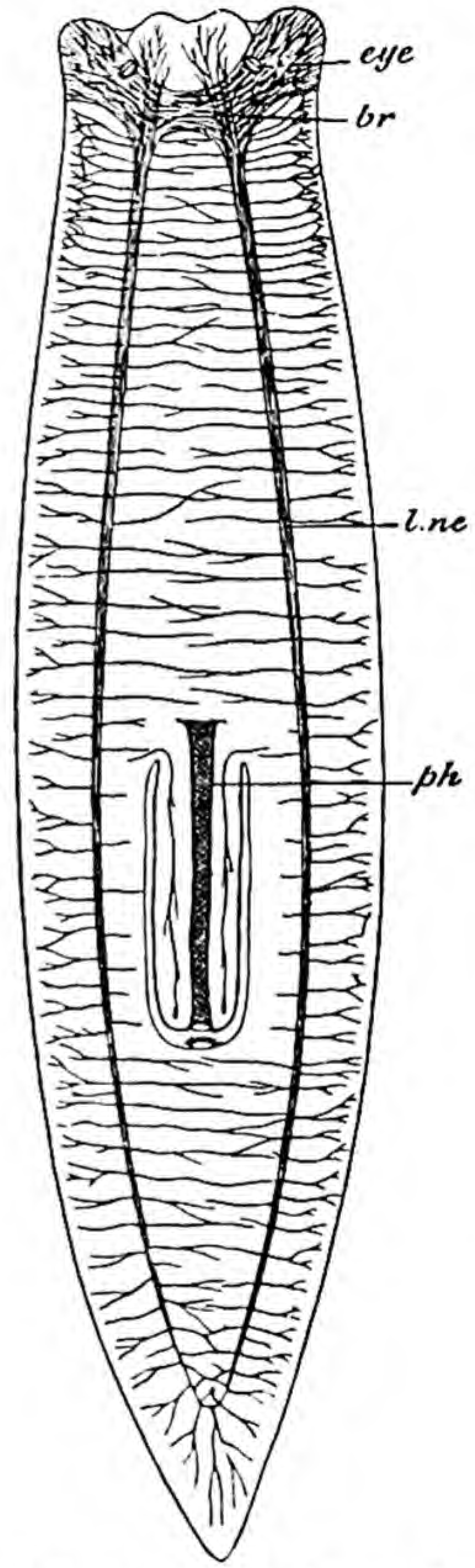


FIG. 184.—**Planaria.** Nervous system. *br.* brain; *eye*, eye; *l. ne.* longitudinal nerve; *ph.* pharynx. (After Jijima and Hatschek.)

means of waves of contraction of the body musculature passing backwards along the body.

Close to the anterior extremity on the dorsal surface are two rounded black

spots, the *eyes* (Fig. 184). On the ventral surface, a considerable distance behind the middle of the body, is the opening of the *mouth* (Fig. 183, *mo.*), and farther back still, near the posterior pointed end, is a smaller median opening, the *genital aperture.*

Body-wall.—The outer covering of the animal consists mainly of ciliated ectodermal cells (Fig. 185). These cells contain so-called *rhabdites*, rod-shaped bodies of a hyaline appearance. On being liberated from the body, the rhabdites, coming into contact with water, swell and stick together, forming a layer of sticky substance around the animal. The function of the rhabdites is not yet satisfactorily understood. It is assumed that they may serve both in the catching of living prey and in the protection of the animal. Among the cells forming the integument glandular and sensory cells are to be found in certain regions of the body. A basal membrane (6) divides the layer of the ectodermal cells from the underlying muscle layers. A layer of circular muscles (1) is followed by longitudinal muscles (8). In addition there is a layer of diagonal fibres (9) which are arranged in two planes at right angles. The longitudinal muscles are most strongly developed on the ventral side of the animal. The parenchyma consists mainly of connective tissue cells, part of which are capable of developing into almost any kind of specialized cell, thus playing an important rôle in regenerating lost or damaged parts of the body. A vast number of glandular cells of an unknown function are also found in the parenchyma.

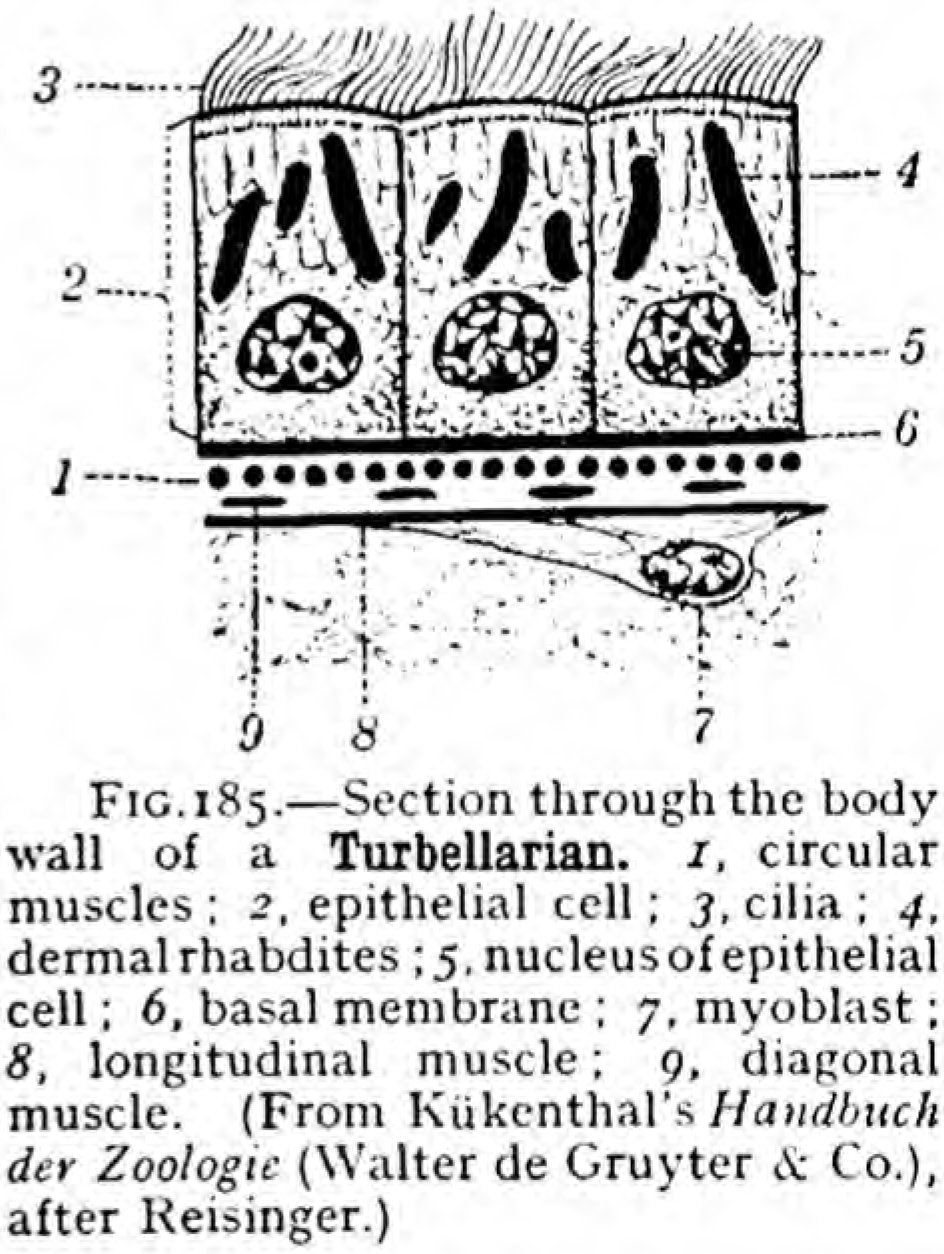


FIG. 185.—Section through the body wall of a **Turbellarian.** *1*, circular muscles; *2*, epithelial cell; *3*, cilia; *4*, dermal rhabdites; *5*, nucleus of epithelial cell; *6*, basal membrane; *7*, myoblast; *8*, longitudinal muscle; *9*, diagonal muscle. (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co.), after Reisinger.)

Digestive System.—The mouth (Fig. 183, *mo.*) leads through a short mouth-cavity into a cylindrical thick-walled chamber, the *pharynx* (*ph.*), which is highly mobile, and is capable of being thrust out as a *proboscis* through the mouth, beyond which it may then be extended to a relatively considerable distance. When retraced it lies within an enclosing muscular *sheath.* The cavity of the pharynx opens in front into the *intestine* (*int.*), which almost immediately divides into three narrow main branches, one running forward in the middle line, the other two running backwards. Each of these three main branches gives off numerous smaller branches, which in turn become branched, so that the whole intestine forms a ramifying system, extending throughout the greater part of the body; all the branches terminate blindly, an anal aperture being absent. The histological structure of the integument of the proboscis is of comparative interest, since here the nuclei of the ciliated epithelial cells have sunk through the basal membrane and through the under-

lying muscles into the parenchyma. Their only connection with their cell bodies consists of long strands of protoplasm. In the *Trematoda* and *Cestoda*, as will be seen later, the entire ectoderm cells have sunk into the parenchyma, lost their cilia, and secreted a thick cuticle which forms the integument of the body (Fig. 190).

A system of vessels—the **water-vessels** or vessels of the *excretory system* (Fig. 183, *ex.*)—sends ramifications through all parts of the body. There are two main, considerably coiled, pairs of longitudinal trunks, right and left, which open externally on the dorsal surface by means of several pairs of minute pores; in front they are connected together by a transverse vessel. The vessels of each pair often join and separate again. Each main trunk gives origin to a number of branches, which in turn give off a system of extremely fine *capillary vessels*, many of which terminate in *flame-cells* (Fig. 186). A flame-cell is a nucleated cell having in its protoplasm a small space into which one of the capillaries leads; in this space lies a bundle of vibratile cilia, which performs regular undulating movements, giving it somewhat the appearance of a flickering candle-flame. Similar bundles of cilia occur also along the branches of the system of water-vessels. By the activity of the ciliary organs the fluid contained in the vessels is moved on towards the excretory pores. Excretory matter is collected from the parenchyma and discharged into the lumen of the water-vessels by a certain kind of glandular cells, the so-called *paranephrocyts*, which are in close contact with the walls of the water-vessels. Besides the removal of excretory waste matters, the system of water-vessels has an *osmoregulatory* function, *i.e.*, it controls the water content of the body.

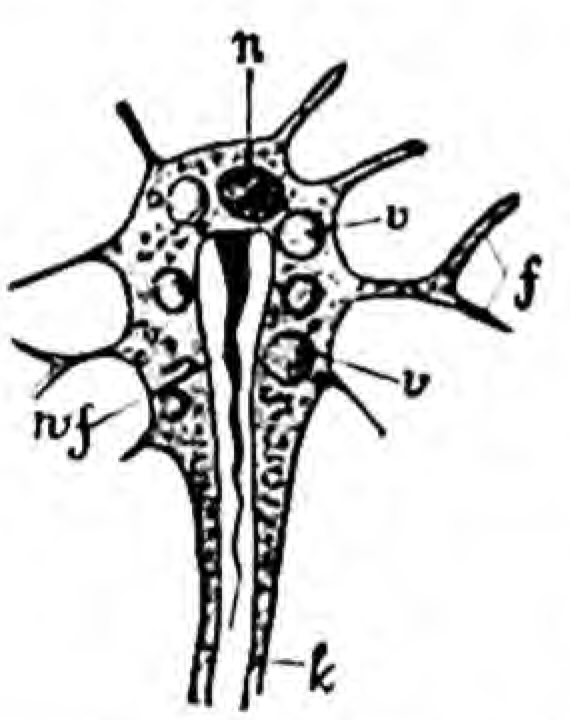


FIG. 186.—Flame-cell of a **Turbellarian.** *f.* processes; *k.* termination of capillary; *n.* nucleus; *v.* vacuoles; *wf.* ciliary flame. (After Lang.)

A well-developed **nervous system** (Fig. 184) is present. At the anterior end is a central knot of nerve-matter, the *brain* (*br.*), from which proceed backwards two *longitudinal nerve-cords* (*l. ne.*). The brain consists partly of transverse fibres connecting together the two longitudinal nerve-cords, partly of groups of nerve-cells situated at the ends, or in the course of, the nerve-fibres. The nerve-cords give off both internally and externally numerous transverse branches, which divide into finer twigs; the internal branches of the two cords frequently anastomose, thus forming *commissures* or connecting nerve-strands between the two. A number of nerves extend forwards to the anterior margin, which is highly sensitive.

The best known of the **sense-organs** are the eyes. They are two rounded dark spots near the anterior end of the dorsal surface. They consist of a cup-like pigment screen the opening of which points laterally forward. Inside the cup, formed by pigment cells, are the sensory cells, which act as light receptors.

The spatial arrangement of the pigment cells and the light-sensitive cells within the pigment screen render the animal capable of a crude discrimination of the direction of the light (Fig. 187).

A variety of sensory cells with various processes are spread over the surface of the body. They are organs of the *chemical* and *mechanical* sense. Groups of sensory cells known as *auricular organs* are arranged at the sides of the head. The cells in these regions are distinguished by the lack of cilia and rhabdites. They are supposed to be organs of the *chemical* sense.

Reproductive System.—The reproductive organs (Fig. 188) are *hermaphrodite* in their arrangement, both male and female organs occurring in the same individual. The genital aperture leads into a small chamber, the *genital atrium*, which is common to both the male and the female reproductive systems.

The male part of the apparatus consists of *testes*, *vasa deferentia*, and *penis*. The testes (*tes.*) are numerous rounded bodies, situated near the right and left borders. Two ducts, the right and left *vasa deferentia* (*v. d.*), run backwards from the neighbourhood of the testes and unite

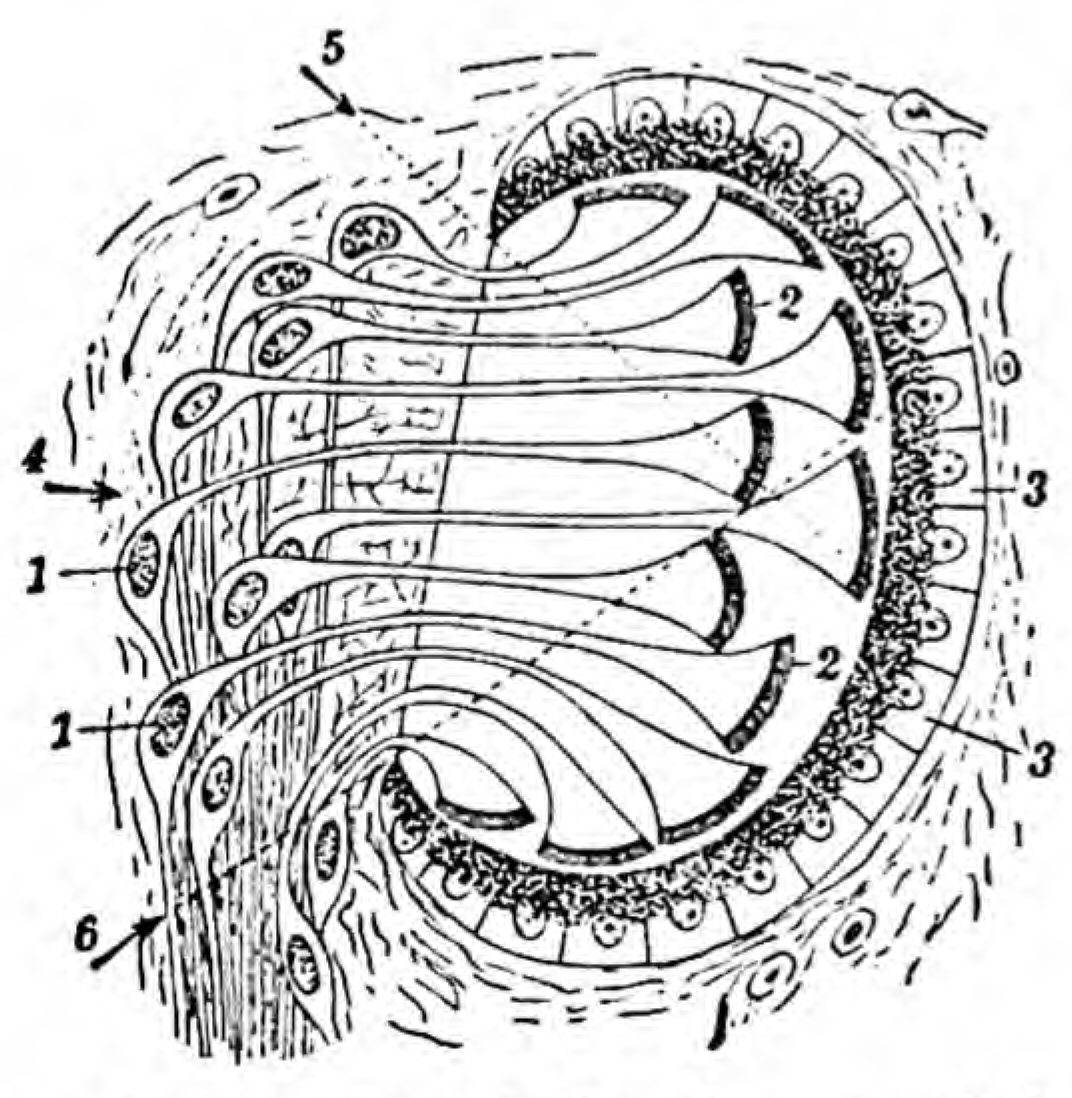


FIG. 187.—Eye of **Planaria gonocephala.** *1*, nuclei of light-sensitive cells; *2*, fibrillæ; *3*, pigment cells; *4*, *5*, and *6*, direction of light rays. Light from *4* stimulates all the sensory cells; light from *5* only those below and light from *6* only those above the broken line. (From Steinmann–Bresslau's *Die Strudelwürmer* (Klinkhardt), after Hesse.)

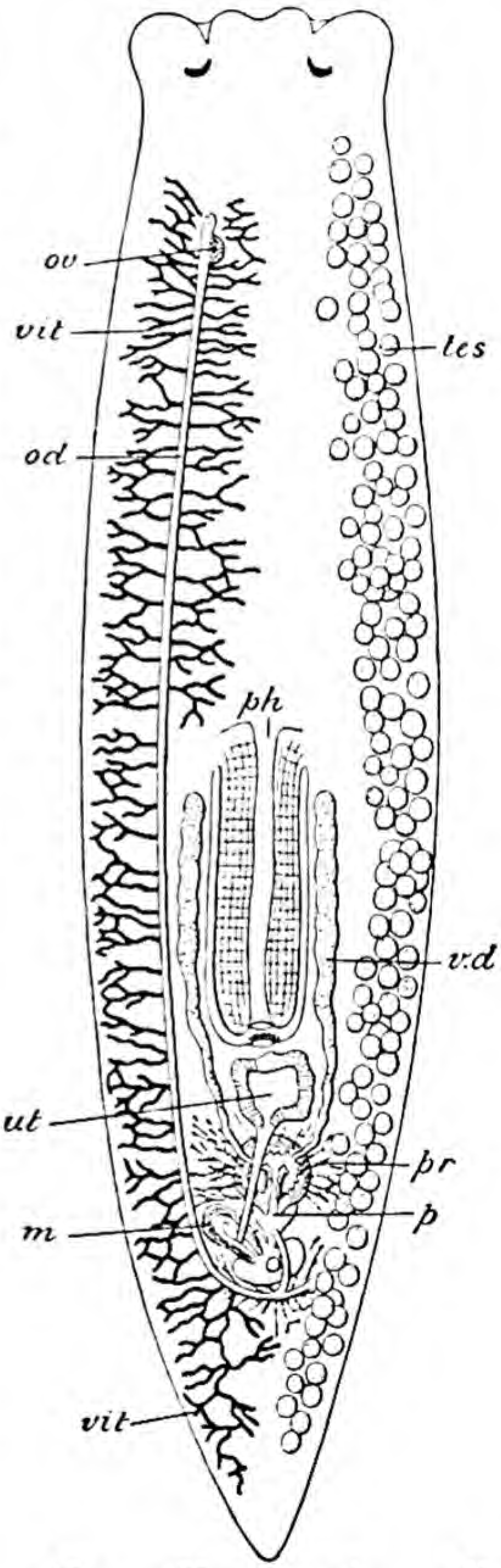


FIG. 188.—**Planaria.** Reproductive system. *m.* muscular sac; od. oviduct; *ov.* ovary (germarium); *p.* penis; *ph.* pharynx; *pr.* prostate; *tes.* testes; *ut.* uterus; *v. d.* vas deferens; *vit.* vitelline glands. (After Jijima and Hatschek.)

in the middle line posteriorly. The median duct formed by the union of the two vasa deferentia traverses a protrusible muscular organ, the *penis* (*p.*), to open into the genital atrium. At the base of the penis, where the vasa deferentia meet, the median canal is slightly enlarged to form a rounded dilatation, the *vesicula seminalis*. Into the median canal open the narrow ducts of a number of unicellular glands, the *prostate glands* (*pr.*).

The female part of the reproductive apparatus consists of *ovaries* (*germaria*), *oviducts*, *vitelline glands*, *uterus*, and *muscular sac*. The *germaria* (*ov.*) are two in number—small rounded bodies situated near the anterior end, each connected with an elongated duct, the *oviduct*. The two oviducts (*od.*) unite posteriorly to form a short median *common oviduct* opening into the genital atrium. With this cavity are connected also the *uterus* (*ut.*), a median rounded chamber, and a thick-walled muscular body, the *muscular sac* (*m.*). Numerous branching tubes—the *vitelline glands* (*vit.*)—open into the oviducts.

Reproduction is entirely sexual. The fertilized egg is enclosed within a protecting case or shell, which contains also a quantity of *food-yolk* derived from the vitelline glands. When the larva has reached a certain stage it develops a temporary larval mouth and gullet, and swallows the food-yolk, by the aid of which it grows rapidly. The larval mouth disappears, and a new one—the permanent mouth—is developed in its place. When the embryo leaves the shell, it has assumed the characteristic shape of the parent.

ii. The Liver-Fluke (*Fasciola hepatica*).

General Features.—The Liver-Fluke of the Sheep, which is to be found in the interior of the larger bile-ducts of the infested animal, is a soft-bodied worm of flattened leaf-like shape (Fig. 189), with a triangular process, the *head-lobe*, projecting from the broader end. The symmetry of the parts is distinctly bilateral, as in the Planarian. Externally the body is quite equilateral, the right and left portions exactly balancing one another, but, as will appear subsequently, this complete symmetry does not extend to all the internal organs.

FIG. 189.—**Fasciola hepatica,** natural size. *excr.* excretory pore; *mo.* mouth; *repr.* reproductive aperture; *sckr.* posterior sucker.

The surface is devoid of vibratile cilia, but is covered with innumerable minute *spinules* or *papillæ*, which are prolongations of the homogeneous external layer or *cuticle* investing the whole animal. At the extreme anterior end of the triangular head-lobe is the small opening of the *mouth* (*mo.*) surrounded by a muscular *oral sucker*. A short distance back on the ventral surface, just behind the head-lobe, is a second much larger *posterior sucker* (*sckr.*). Between the two suckers, but rather nearer the posterior one, is a median aperture, the *genital opening* (*repr.*), through which a curved muscular

process, the *cirrus* or *penis*, may be protruded. In the middle of the posterior end of the body is a minute opening, the *excretory pore* (*excr.*).

Body-wall.—The body-wall (Fig. 190) is found on section to comprise three layers: (1) a homogeneous *cuticle* (*cu.*) of which the spinules (*sp.*) are special developments; (2) a layer of circularly disposed muscular fibres (*circ. m.*); (3) a layer of longitudinal muscular fibres (*long. m.*). A cellular epidermis proper is lacking. The ectodermal cells (*ect. c.*) have sunk into the parenchyma, where they are found close to the layer of longitudinal muscles. They are connected with the cuticle by protoplasmatic processes. Beneath the muscles

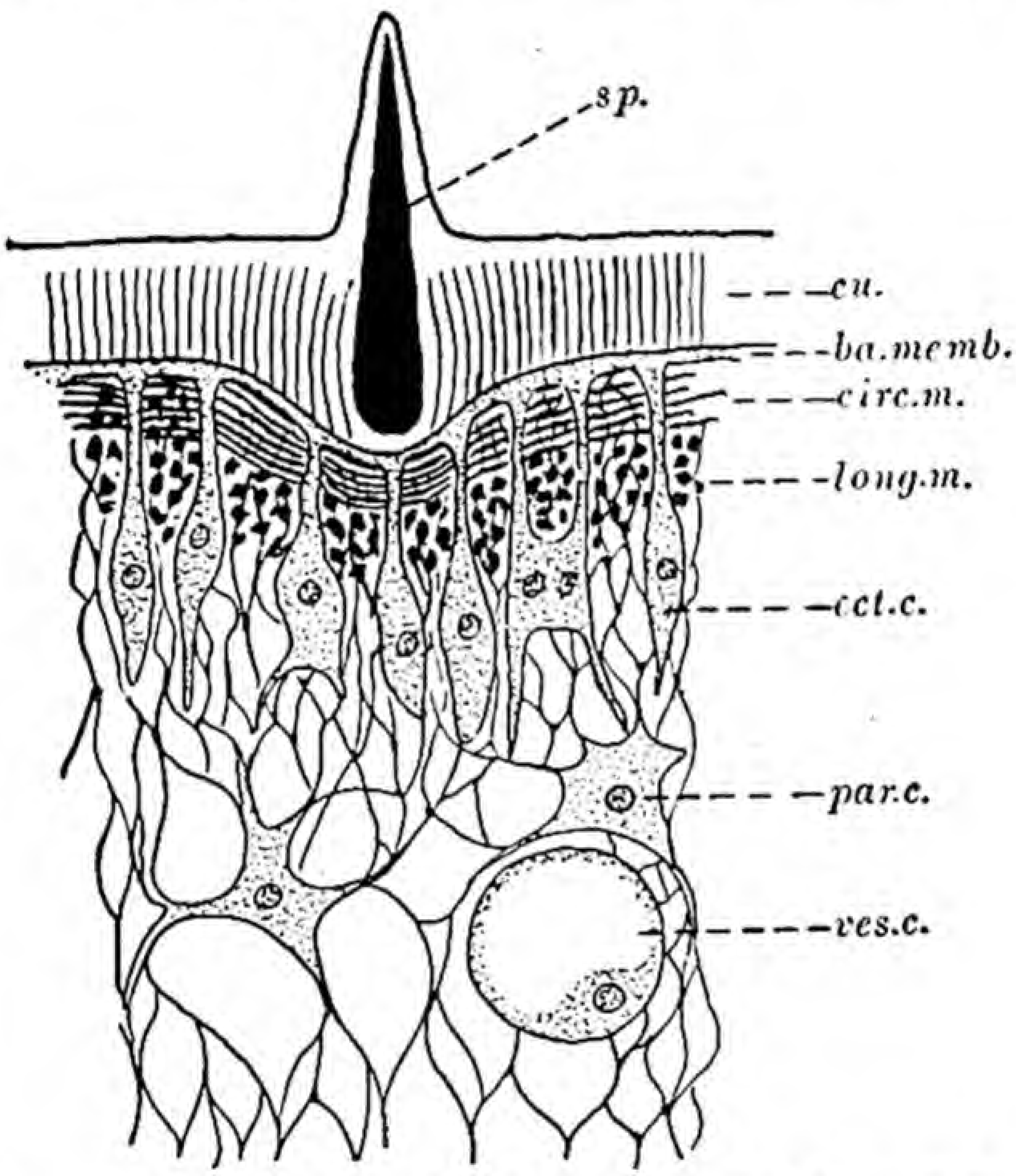


FIG. 190.—Transverse section through the body wall of a **Trematode.** *ba. memb.* basement membrane; *circ. m.* circular muscle layer; *cu.* cuticle; *ect. c.* ectoderm cell; *long. m.* longitudinal muscle layer; *par. c.* parenchyma cell; *sp.* spinule; *ves. c.* vesicular cell. (From Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge), after Benham.)

are numerous *unicellular glands*, the ducts of which, open on the outer surface. Internally, the interspaces between the organs are filled by the *parenchyma*.

Digestive System.—The mouth (Fig. 191) leads to a small rounded bulb-like body, the *pharynx* (*ph.*), with thick muscular walls and a small cavity. From this a short passage, the *œsophagus*, opens into the *intestine*. The latter (*int.*) is frequently a very conspicuous structure, owing to its being filled with the dark biliary matter mixed with blood on which the Fluke feeds. It divides almost immediately into two main limbs, right and left, and from each of these are given off, both internally and externally, a number of blind branches or *cæca*, those on the inner side being short and simple, while those on the outer side are longer and branched. The two limbs of the intestine

with their branches thus form, as in the Planarian, a complicated system, the ramifications of which extend throughout the whole of the body. There is no aperture of communication between the intestine and the exterior, the only external opening of the alimentary system being through the mouth.

A branching system of vessels—the **water-vessels** or vessels of the **excretory system**—ramify throughout the body. A longitudinal *main trunk* opens behind

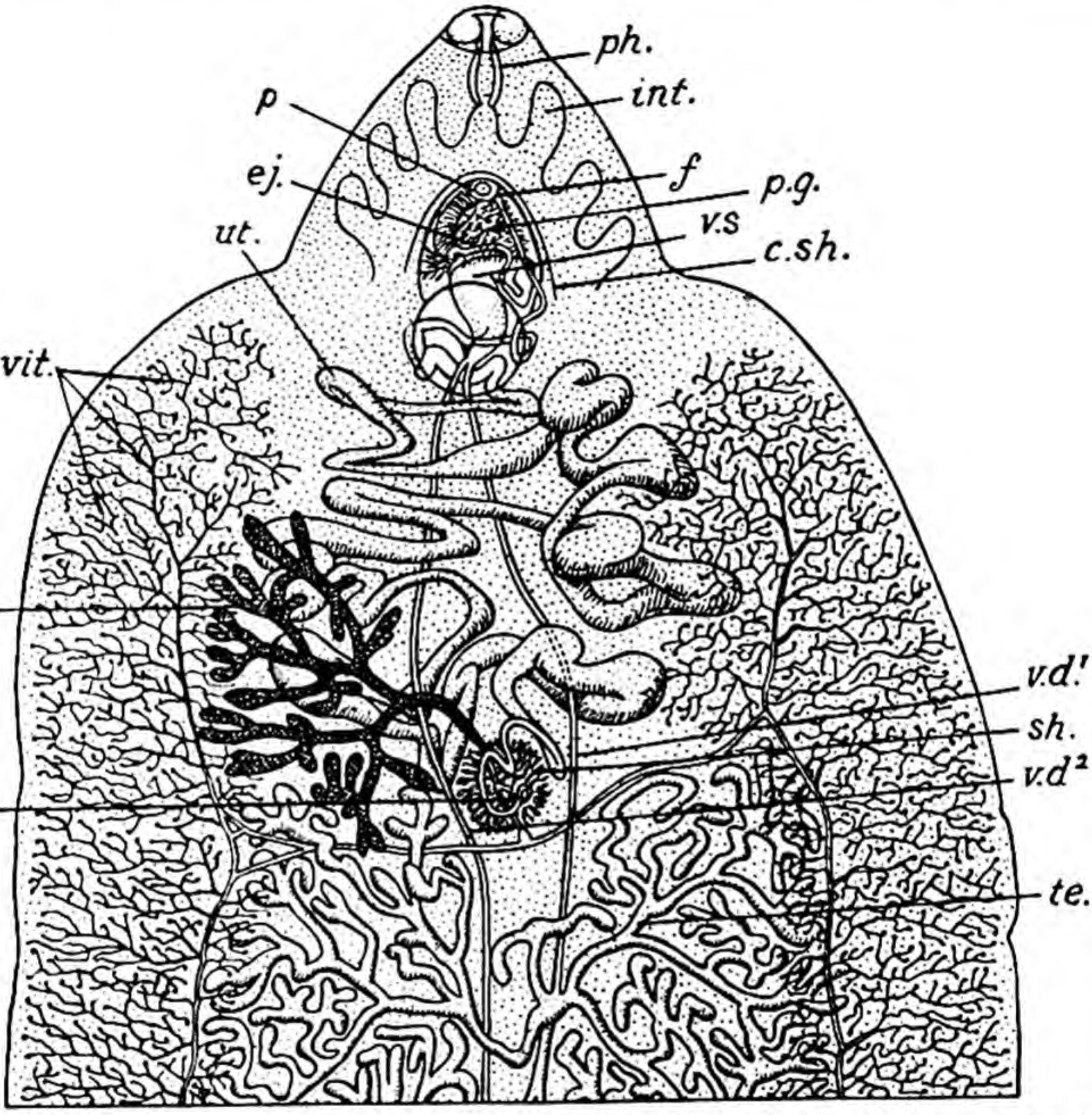


FIG. 191.—**Fasciola hepatica.** Internal organization. General view of the anterior portion of the body, showing the various systems of organs as seen from the ventral aspect. *c. sh.* cirrus sheath; *ej.* ejaculatory duct; *f.* female reproductive aperture; *int.* anterior portion of the intestine (the rest is not shown); *od.* commencement of oviduct; *ov.* ovary (germarium); *p.* cirrus; *p. g.* prostate gland; *ph.* pharynx; *sh.* shell-gland; *te.* testes; *ut.* uterus; *v.* d_1. left vas deferens; *v.* d_2. right vas deferens; *vit.* lobes of vitelline glands; *v. s.* vesicula seminalis. (After Sommer.)

by means of the excretory pore already mentioned as occurring at the posterior end. In front it gives off four large trunks, each of which branches repeatedly, the branches giving off smaller vessels, and these again still smaller twigs, until we reach a system of extremely fine microscopic vessels or *capillaries*. Each of these ends internally in a slight enlargement situated in the interior of a large *flame-cell*, similar to a flame-cell of the Planarian.

The Liver-Fluke has a well-differentiated **nervous system**, which shares in the prevailing bilateral arrangement of the parts. The central part of this system consists of a ring of nerve-matter which surrounds the œsophagus and presents two lateral thickenings, or *ganglia*, containing nerve-cells, and a single ganglion in the middle line below. From this are given off a number of nerves, of which the chief are a pair of *lateral cords* running back to the posterior end and giving off numerous branches. In consequence of the parasitic mode of life, proper sense-organs are absent.

The **reproductive organs** (Fig. 191) are constructed on the hermaphrodite plan, *i.e.*, both male and female organs occur in the same individual. The male part of the apparatus consists of *testes*, *vasa deferentia*, and *cirrus*. The *testes* (*te.*), are two greatly ramified tubes, which occupy the middle part of the body, one situated behind the other. From each testis there runs forwards a duct, the *vas deferens*, the two vasa deferentia (*v. d.*) opening anteriorly into an elongated sac, the *vesicula seminalis* (*v. s.*), from which a narrow tube—the *ejaculatory duct* (*ej.*)—leads to the male aperture at the extremity of the cirrus. The female part of the reproductive apparatus consists of a single *ovary* (*germarium*), an *oviduct*, a *uterus*, an *ootype*, *vitelline glands*, *vitelline ducts*, and "*shell-glands*." The *germarium* (*ov.*) is a branched tube situated on the right-hand side in front of the testes; the branches open into a common narrow tube, the *oviduct* (*od.*). The *vitelline glands* (*vit.*) consist of very numerous, minute, rounded follicles, which occupy a considerable zone in the lateral regions of the body. On each side are two large ducts, anterior and posterior, uniting to form a single main lateral duct, right or left; and these run nearly transversely inwards to open into a small sac, the *yolk reservoir*. From this a single median *vitelline duct* runs forwards for a short distance to join the oviduct. Around the junction are grouped a mass of unicellular *shell-glands* or *accessory female glands* (*sh.*), each of which is produced into a narrow process or duct opening into the end of the oviduct in the region of the latter to which the term *ootype* is applied. The *uterus* (*ut.*) is a wide convoluted tube, formed by the union of the oviduct and median vitelline duct; in front it opens close to the base of the cirrus. When the cirrus is withdrawn, a small cavity, the *genital atrium*, is formed, common to the external apertures of both male and female ducts. A canal, termed the *canal of Laurer*, leads from the junction of the oviduct and median vitelline duct to open externally on the dorsal surface.

Development.—Each ovum on fertilization is surrounded by a mass of vitelline matter or *yolk* derived from the yolk-glands. It then becomes enclosed, while passing through the ootype, in a chitinous shell, the substance of which is derived from the yolk, the formation of the shell being aided by a secretion of the shell-gland. The completed egg remains for a little time in the uterus; eventually it is discharged, and, passing down the bile-ducts of the Sheep into the intestine, reaches the exterior with the fæces. Active

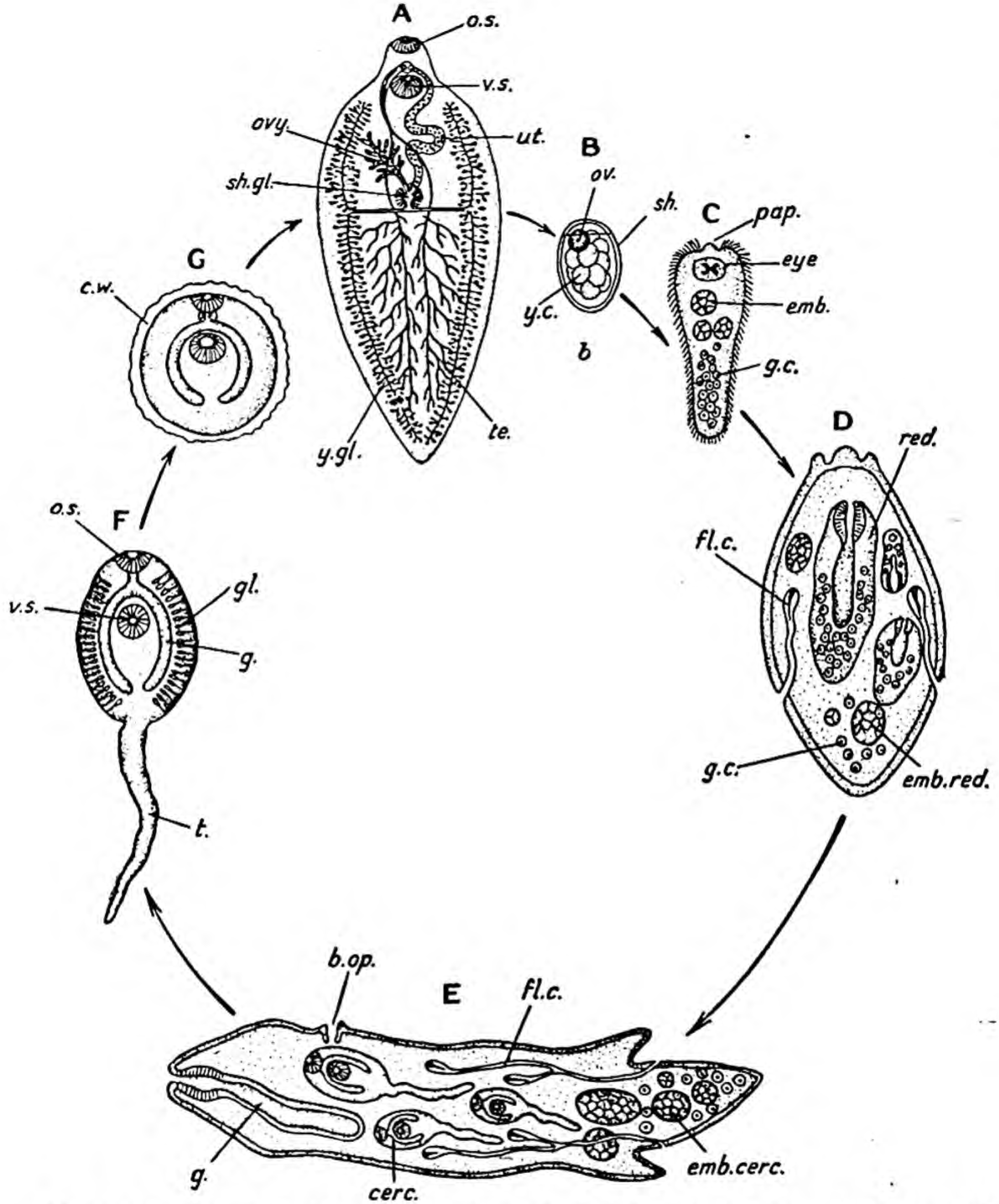


FIG. 192.—Life-history of **Fasciola hepatica.** *A*, adult Fasciola hepatica; *B*, egg case with ovum; *C*, Miracidium; *D*, sporocyst with rediæ; *E*, redia with cercariæ; *F*. cercaria; *G*, encysted cercaria; *b. op.* birth opening; *cerc.* cercaria; *c. w.* cyst wall; *emb.* embryo; *emb. cerc.* embryo of cercaria; *emb. red.* embryo of redia; *fl. c.* flame cells; *g.* gut; *g. c.* germ cells; *gl.* glands; *o. s.* oral sucker; *ov.* ovum; *ovy.* ovary; *pap.* papilla; *red.* redia; *sh.* shell; *sh. gl.* shell gland; *t.* tail; *te.* testis; *ut.* uterus; *v. s.* ventral sucker; *y. c.* yolk cells; *y. g.* yolk glands. (From Kühn's *Grundriss der Allgemeinen Zoologie, 5. Auflage* (Verlag Georg Thieme, Leipzig, 1936), modified.)

development only begins at this stage, and three to six weeks later a portion of the egg-shell at one end becomes separated off as a sort of lid or *operculum*, and gives exit to the contained embryo. This, the *ciliated embryo* or *miracidium* (Fig. 192, *C*), is a somewhat conical body, covered all over with vibratile cilia, and there are two spots of pigment, the *eye-spots* (*eye*), near the broader or anterior end, which is provided with a triangular head-lobe (*pap.*). There is an imperfectly developed intestine, and a pair of flame-cells, each with a fine canal opening on the surface. The rest of the interior is filled with a mass of germ-cells. The ciliated larva swims about in water, or moves over damp herbage for a time, and perishes unless it happens to reach a water-snail (species of *Limnæa*, or of *Bulinus* or *Planorbis*), as a parasite of which it is alone able to enter upon the next phase in its life-history. When it meets with the Snail, the embryo bores into it by means of the head-lobe, coming to rest in the pulmonary sac or some other organ of the mollusc. Established in the interior of the Snail, it loses its ectoderm and grows rapidly into the form of an elongated sac, the *sporocyst* (Fig. 192, *D*), with an internal cavity containing germ-cells and lined by a layer of cells, with remnants of the eye-spots, and with flame-cells. The sporocyst may divide into two similar bodies by a process of transverse fission, but this is exceptional. Eventually cells are budded off from the layer that lines the internal cavity of the sporocyst or from the germ-cells, and these undergo a process of cleavage similar to the holoblastic cleavage of the fertilized ovum, resulting in the formation of a morula, which becomes converted into a stage resembling a gastrula. The gastrula elongates and gives rise to a body called a *redia* (*E*), which begins to move about, and, eventually forcing its way out of the interior of the sporocyst, finds its way to some other part of the Snail, usually the liver. When fully formed, the redia is a cylindrical body with a pair of short processes near the posterior end, and with a circular ridge near the anterior end. It possesses a mouth leading to a pharynx and simple sac-like intestine, and there is a system of excretory vessels. In the interior of the redia cells are budded off and develop into gastrulæ, exactly as in the case of the sporocyst; these gastrulæ either develop into a fresh generation of rediæ if the season should be winter, or, if it should be summer, give rise to bodies termed *cercariæ*. The latter (*F*) are provided with long tails: they have anterior and posterior suckers, and a mouth and pharynx, followed by a bifid intestine. An opening, the *birth-opening* (*E, b. op.*), is formed in the wall of the redia near the circular ridge, and through this the cercariæ escape; they move actively by means of their tails, and force their way out of the body of the Snail. They then, losing the tail, become encysted (*G*), attached to blades of grass or leaves of other herbage. The transference of the larval Fluke in this stage to its final host, the Sheep, is effected if the latter swallow the grass on which the cercaria has become encysted. The young Fluke then escapes from the cyst and forces its way

up the bile-ducts to the liver, in which it rapidly grows, and, developing reproductive organs, attains the adult condition.

iii. The Common Tape-Worm of Man (*Tænia solium*).

General Features.—*Tænia solium* occurs as a parasite in the intestine of Man. It has the form of a narrow ribbon (Fig. 193), which may attain a length of several yards, attached at one end to the wall of the intestine, the remainder hanging freely in the interior. Towards the attached end the ribbon becomes very much narrower than it is towards the opposite end; and at this narrower extremity is a small, rounded, terminal knob, which is known as the *head* or *scolex*; the rest of the animal is termed the *body* or *strobila*; the narrow part immediately behind the head is sometimes called the *neck*. The attachment of the Tape-worm to the wall of the intestine is slight and temporary; it is effected by certain organs of adhesion, the *hooks* and *suckers* on the head.

The *head* (Fig. 194) may be roughly described as pear-shaped, but becomes

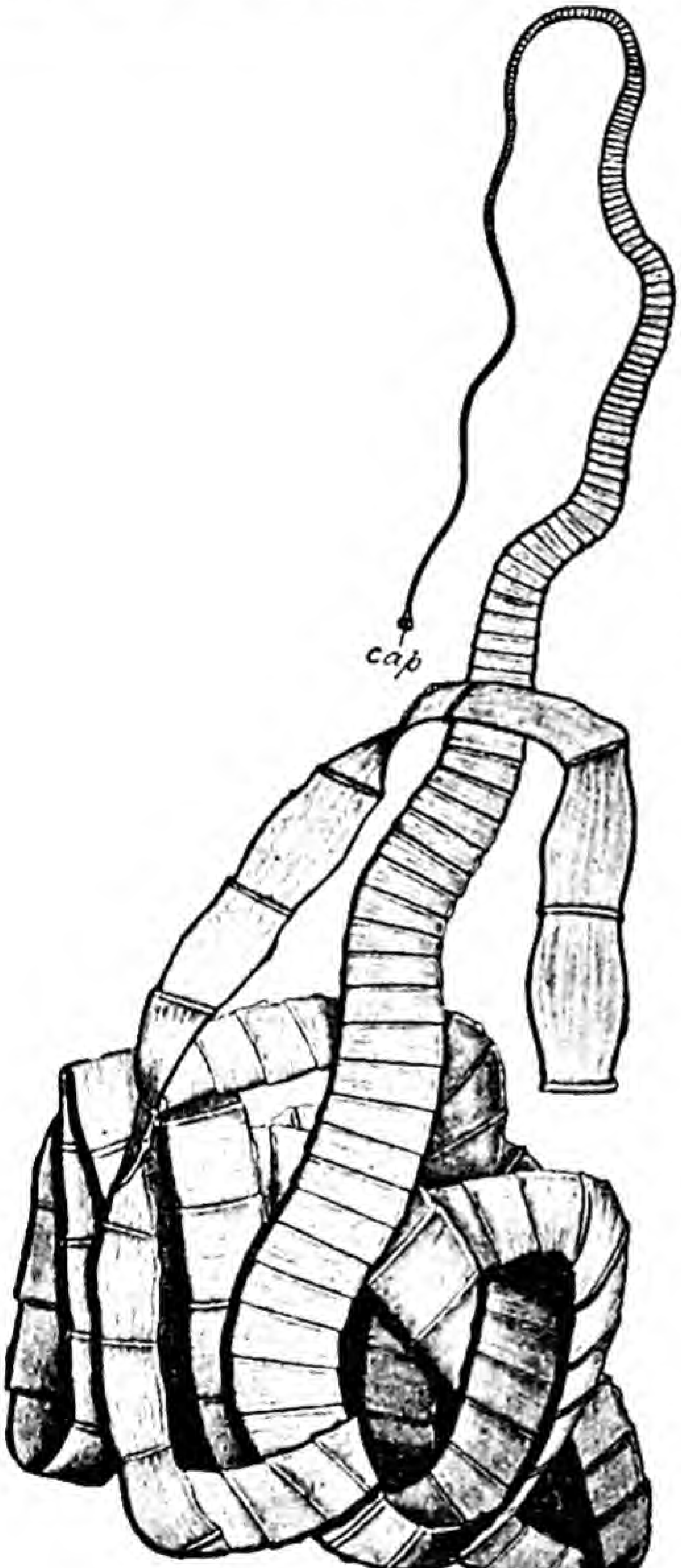


FIG. 193.—**Tænia solium.** Entire specimen, reduced; *cap.* head. (After Leuckart.)

FIG. 194.—**Head of Tænia solium,** magnified. (After Leuckart.)

four-sided at the broader end. In the middle of this broader, anterior end is a rounded prominence, the *rostellum*, round the base of which there is a double row of usually about twenty-eight curved and pointed chitinous hooks. The

rostellum is capable of being protruded and retracted to a slight extent, and the position of the hooks varies accordingly: when the rostellum is fully retracted the points of the hooks are directed forwards, and may even meet in the centre; as the rostellum is protruded the hooks become rotated until their apices come to be directed backwards. Four cup-shaped suckers project slightly from the surface behind the circlet of hooks.

The *body* or *strobila* has a jointed appearance, owing to its being made up of a string of segments, or *proglottides*—about 850 altogether. These are narrower and shorter in front, gradually increasing in size towards the posterior free extremity. The *neck*, the part immediately following the head, is devoid of any trace of segmentation. The two surfaces of the proglottides are not to be distinguished by any differences visible to the unassisted eye; but that

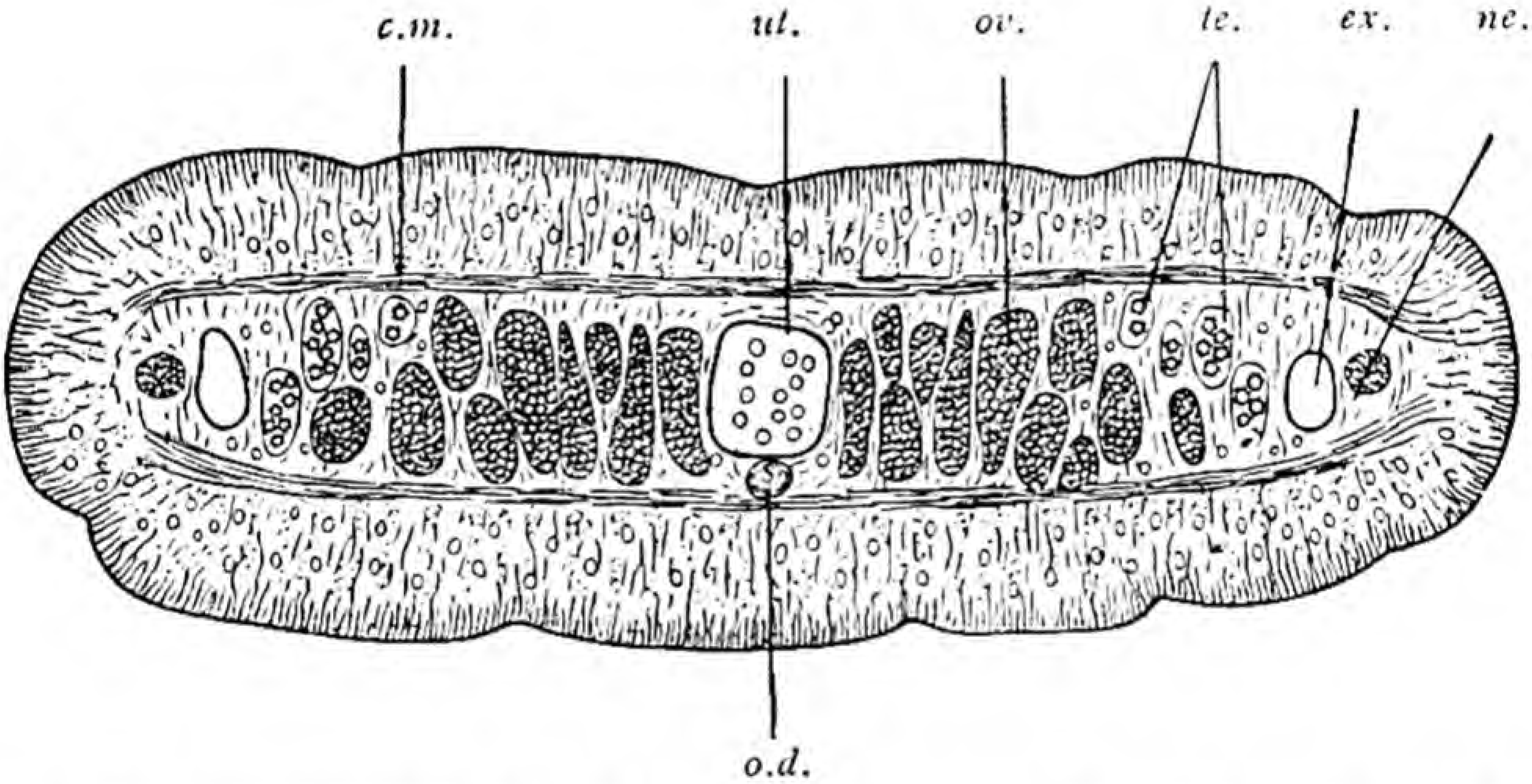


FIG. 195.—Transverse section of **Tænia solium.** *c. m.* circular layer of muscle; *ex.* longitudinal excretory vessel; *ne.* longitudinal nerve; *od.* oviduct; *ov.* ovary; *te.* testes; *ut.* uterus. (After Shipley.)

side towards which the female reproductive organs are more nearly approximated is regarded as the *ventral*, the opposite as the *dorsal* surface. On one border, alternately on the right and left of each proglottis, is a little prominence, the *genital papilla*, on which is the opening of a chamber, the *genital atrium*, into which both the male and female reproductive ducts open.

The body is covered by a thick cuticle which is secreted by ectoderm cells sunk into the parenchyma. Underlying the cuticle is a layer of longitudinal muscles. It is followed by a layer of circular muscles which divides the parenchyma into an outer *cortical* and an inner *medullary* region. The latter contains the nervous system and the organs of excretion and reproduction.

An examination of entire living and of preserved and stained Tape-Worms under the microscope shows (1) that an alimentary system is not present; (2) that nervous and excretory systems are represented; (3) that there is a

complete set of reproductive organs, present in each of the proglottides, and constructed on the same general plan as those of the Liver-Fluke.

The **nervous system** consists of two not very well-defined *ganglia* situated in the head and united by a broad transverse commissure of slender nerves passing from these to the suckers, and of two *longitudinal nerves* which run backwards through all the proglottides to the posterior end of the body. The ganglia seem to correspond to the ganglia on the nerve-ring of the Liver-Fluke.

The **excretory organs** consist of a richly branched system of excretory vessels. There are four *main longitudinal trunks* (Fig. 196, *can. excret.*), two near each lateral margin in the more anterior part of the strobila; in the more posterior region one of these becomes lost on each side. The two pairs of longitudinal vessels are connected together in the head by a ring-like vessel and in each proglottis near its posterior margin by a straight, transverse, connecting branch. Posteriorly the longitudinal trunks open into a pulsatile *caudal vesicle*, communicating with the exterior in the last proglottis. When the latter becomes thrown off, the vesicle is lost with it, and, subsequently, the longitudinal vessels have their separate openings on the exterior. These main trunks of the excretory system give origin to a number of branches, and these in turn give off numerous fine canalicules, or capillaries, terminating in flame-cells, similar to those of the Fluke.

The **reproductive organs** (Fig. 196), repeated in each fully formed proglottis, are in essential respects very similar to those of the Liver-Fluke. In the most anterior proglottides they are not developed; it is only at about the 200th proglottis that they first appear: at first the male parts of the system are alone differentiated; then in the succeeding proglottides, till we approach the posterior extremity of the body, the female organs are likewise developed. In the most posterior segments modifications and reductions of some of the parts take place, owing to the great increase in size of the uterus. The male portion of the apparatus consists of the *testes* with their *efferent ducts*, the *vas deferens* (*vas. def.*), and the *cirrus*, with its *sac*. The *testes* consist of numerous rounded lobes situated nearer the dorsal than the ventral surface, and extending throughout the greater part of the length and breadth of the proglottis. With each lobe is connected a fine *efferent duct*; the ducts of neighbouring lobes unite together to form somewhat larger ducts; and the larger ducts, receiving numerous tributaries, eventually open into the inner extremity of the *vas deferens*, or main duct of the testis. The *vas deferens* is a convoluted tube which extends outwards towards the lateral margin (right or left as the case may be) of the proglottis.

The terminal part of the vas deferens, which is somewhat narrower than the rest, traverses a narrow protrusible process, the *cirrus*, and opens at its extremity by the *male genital aperture* in the genital *atrium*. The cirrus is enclosed at the base by a muscular sac, the *cirrus-sac*.

The *ovary* (*germarium*) (*ov.*) differs from that of the Liver-Fluke in being a paired organ, consisting of two approximately equal, right and left, halves. It is situated towards the posterior border of the proglottis. Like that of the Liver-Fluke, it consists of a number of branching tubes, in the interior of which the ova are developed. From opposite sides these tubes converge towards the median line, where they open into the *oviduct*. A *yolk-gland* (*gl. vit.*), of less relative extent than in the Liver-Fluke, consists of a number of minute lobules; a duct, the *yolk-duct*, which runs forward from it, opens into the oviduct. The numerous lobules of a rounded "*shell-gland*" (*sh.g.*)

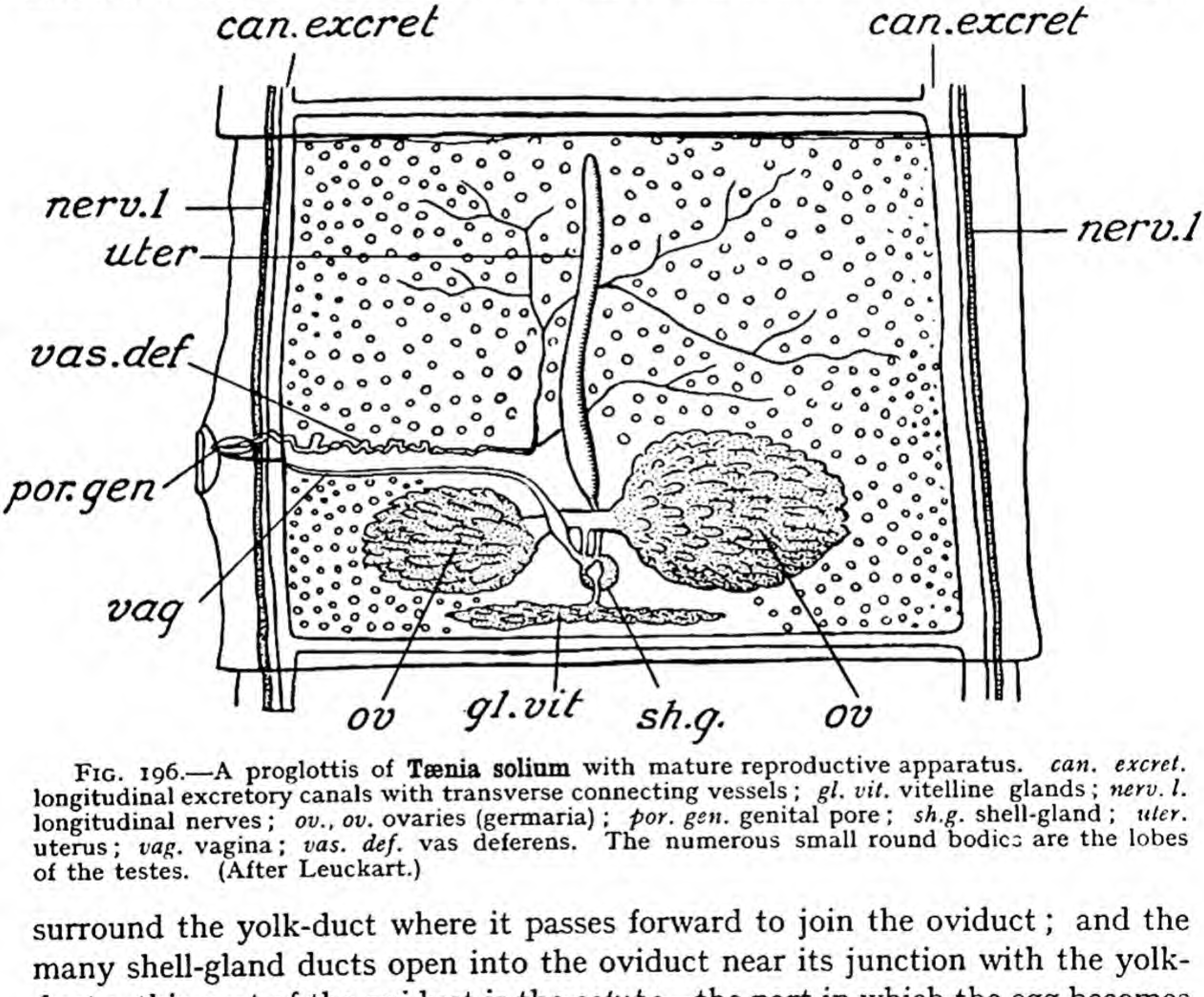


FIG. 196.—A proglottis of **Tænia solium** with mature reproductive apparatus. *can. excret.* longitudinal excretory canals with transverse connecting vessels; *gl. vit.* vitelline glands; *nerv. l.* longitudinal nerves; *ov.*, *ov.* ovaries (germaria); *por. gen.* genital pore; *sh.g.* shell-gland; *uter.* uterus; *vag.* vagina; *vas. def.* vas deferens. The numerous small round bodies are the lobes of the testes. (After Leuckart.)

surround the yolk-duct where it passes forward to join the oviduct; and the many shell-gland ducts open into the oviduct near its junction with the yolk-duct: this part of the oviduct is the *ootype*—the part in which the egg becomes completed. In front this passes into the *uterus*. The female genital pore, situated in the genital atrium, leads into a narrow passage, the vagina, which runs inwards and backwards towards the middle line of the proglottis, where it ends in a dilatation usually filled with sperms—the *receptaculum seminis*. From this a narrow duct—the *fertilizing duct* or *spermatic duct*—runs to join the oviduct. The *uterus*, in the segments in which it first makes its appearance, is a simple cylindrical diverticulum of the oviduct; it retains its simple form

as far back as about the 600th proglottis, where it begins to branch, the ramifications increasing in extent and volume in the posterior segments. It has no opening on the exterior.

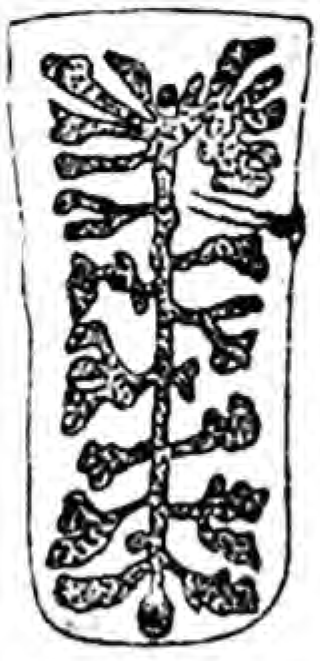


FIG. 197.—"Ripe" proglottis of **Tænia solium**. (After Leuckart.)

Masses of sperms (probably from the same proglottis) pass in the act of copulation along the vagina to the *receptaculum seminis*; through the fertilizing duct they pass to the oviduct to fertilize the ova. As in the case of the Liver-Fluke, the fertilized egg becomes surrounded by a quantity of food-yolk developed in the yolk-glands, and is then enclosed in a firm chitinous shell supposed to be formed by the secretion of the shell-gland. It then passes into the uterus. The first completed eggs are found in the uterus in some proglottis between the 400th and the 500th. From this point backwards they rapidly accumulate, until the cavity of the uterus, which now becomes branched, is filled and distended with them. Eventually in the most posterior, so-called "ripe," proglottides (Fig. 197), the uterus, with its contained accumulation of eggs, becomes so large as

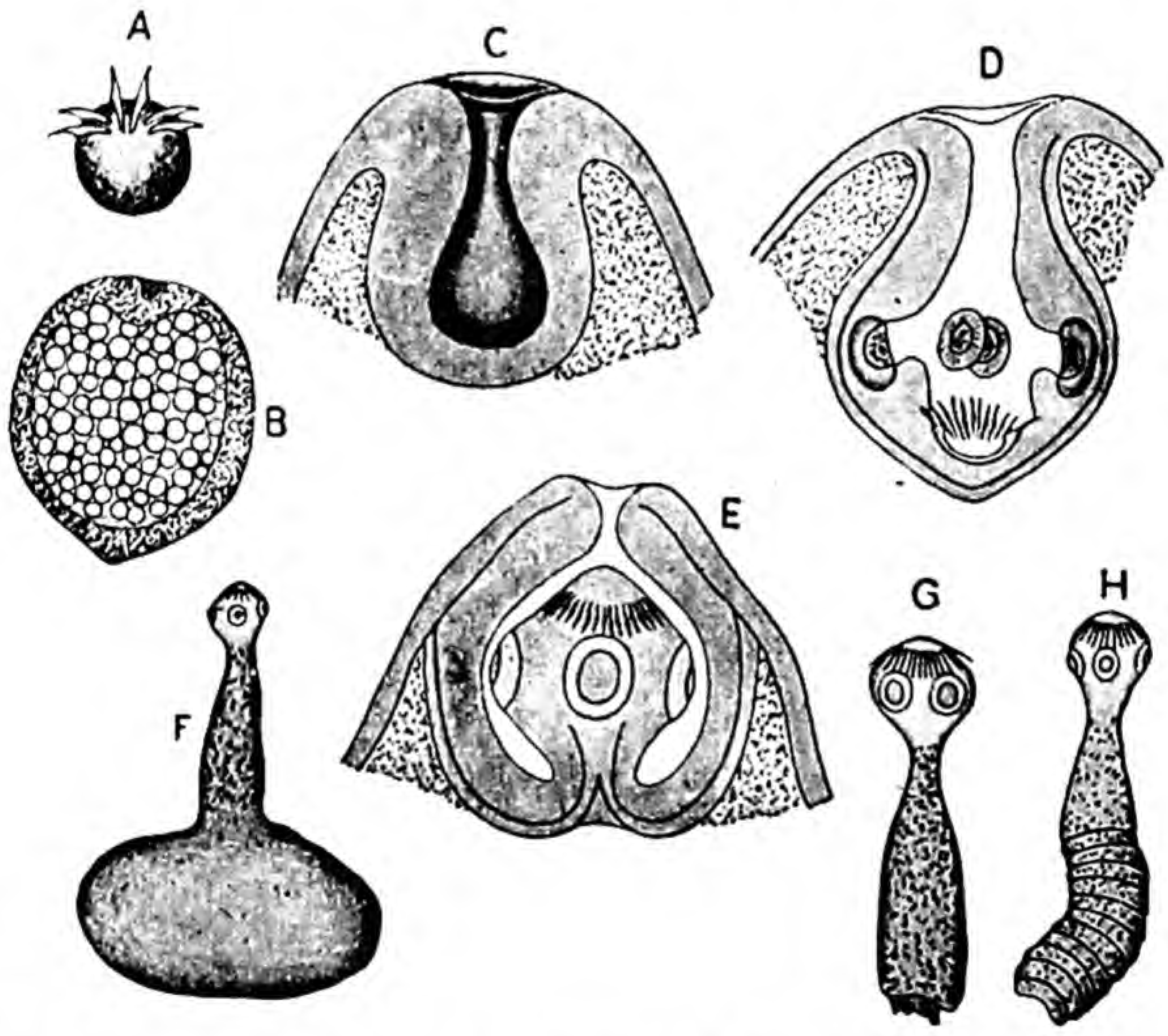


FIG. 198.—Development of **Tapeworm**. *A* six-hooked embryo; *B*, early stage of bladder-worm of *Tænia* sp.; *C*—*E*, stages in the formation of the scolex of the same; *C*, the invagination before the hooks and suckers have become developed; *D*, after the appearance of the hooks and suckers; *E*, partly evaginated; *F*, fully evaginated scolex of *T. solium* with caudal vesicle; *G*, scolex of *T.* serrata with remains of the vesicle; *H*, young tapeworm of *T.* serrata. (After Leuckart.)

to fill the greater part of the interior of the proglottis, the remainder of the reproductive apparatus meanwhile having become absorbed.

Development.—When the ripe proglottides are detached they pass to the exterior with the fæces of the host. For a time they exhibit movements of contraction. The embryos contained within the eggs have meantime assumed the form of rounded bodies, each armed with six chitinoid hooks—the *six-hooked embryo* or *proscolex* enclosed within two membranes. If the proglottides, or the eggs which have escaped from them, should now be taken into the alimentary canal of the Pig, which forms the ordinary second host of the parasite, the hooked embryos, becoming freed from their coverings (Fig. 198, *A*) bore their way with the aid of their hooks through the wall of the alimentary canal, and reach the voluntary muscles. Here they increase greatly in size, and develop into rounded cysts with a large cavity filled with watery fluid (*B*.) On the wall of the bladder, at one side, is formed a hollow ingrowth, or invagination (*C*); and on the inner surface of this are developed the hooks and suckers characteristic of the head or scolex of the adult (*D*). When these are fully formed the hollow ingrowth becomes everted (*E*), the suckers and hooks thus coming to be situated on the outer surface (*F*). The whole embryo has now the form of a bladder or vesicle, with which is connected at one point a process having all the characters of the head and neck of the mature Tænia solium; this is the bladder-worm stage, or *cysticercus*. If a portion of Pig's muscle containing *cysticerci* which have not been killed by cooking is taken into the stomach of Man, the bladder is thrown off, the scolex attaches itself to the wall of the intestine by its hooks and suckers, and develops the series of proglottides of the adult Tape-Worm.

2. Distinctive Characters and Classification.

The Platyhelminthes are bilaterally symmetrical, usually dorso-ventrally compressed animals, devoid of hard supporting skeleton—either external or internal—and also of metameric segmentation; with three embryonic layers—ectoderm, mesoderm, and endoderm—entering into the formation of the body. A body-cavity is not present. There is a system of excretory vessels, communicating in the majority of cases with the exterior, and furnished with ciliary flames. There is no blood-vascular system. An enteric cavity may be absent, may be rudimentary, or may be highly developed; it is very rarely provided with an anal aperture. The completed egg contains, in addition to the zygote, a quantity of yolk-matter, usually in the form of definite yolk-cells, and usually produced by a special set of yolk-glands. Development is sometimes direct, sometimes accompanied by a metamorphosis.

CLASS I.—TURBELLARIA.

Mostly non-parasitic Platyhelminthes with ciliated cellular epidermis; with a digestive cavity.

ORDER I.—ACŒLA.

Small Turbellaria without proper pharynx and gut. Mouth leads directly into the central region of the parenchyma in which digestion takes place.

Example: *Convoluta* (Fig. 199).

ORDER 2.—RHABDOCŒLA, *incl.* TEMNOCEPHALIDÆ.

Comparatively small Turbellaria, with the body usually elongate and cylindrical or compressed: with simple, or nearly simple, sac-like intestine; with or without yolk-glands; with one or two ovaries and two or many testes. Examples: *Mesostoma* (Fig. 216), *Dalyellia* (*Vortex*) (Fig. 199), *Microstomum* (Fig. 228). The order includes also the *Temnocephalidæ*; living on the outer surface or in the respiratory cavities of various fresh-water animals—*e.g.*, Crustaceans; non-parasitic as regards their nutrition; with a single posterior sucker and a system of anterior or marginal tentacle-like appendages.

Examples: *Temnocephala* (Fig. 200), *Actinodactylella* (Fig. 201).

ORDER 3.—TRICLADIDA.

Turbellaria with elongate depressed body; with numerous yolk-glands, two ovaries, numerous testes; a single genital aperture; intestine consisting of a median anterior division and two lateral posterior limbs which are provided with side branches.

Examples: *Bipalium* (Fig. 199), *Polycelis* (Fig. 199), *Procerodes* (Fig. 202), *Rhynchodemus* (Fig. 199).

ORDER 4.—POLYCLADIDA.

Flattened leaf-shaped Turbellaria, without separate yolk-glands; testes and ovaries numerous; male and female genital apertures usually separate; intestine complexly branched.

Examples: *Thysanozoon* (Fig. 199), *Planocera* (Fig. 218).

CLASS II.—TREMATODA.

Ecto- or endoparasitic Platyhelminthes devoid of cilia, or of a cellular epidermis; with a well-developed digestive apparatus.

ORDER I.—MONOGENA (HETEROCOTYLEA).

Mostly ectoparasitic Trematodes; with direct development.

Examples: *Gyrodactylus* and *Polystomum* (Fig. 203).

ORDER 2.—DIGENA (MALACOCOTYLEA).

Endoparasitic Trematodes generally with complicated life-history.

Examples: *Amphistomum* (Fig. 204), *Lophotaspis* (Fig. 205), *Gastrodiscus* (Fig. 206), *Fasciola* (Fig. 191), *Schistosomum* (Fig. 229).

CLASS III.—CESTOIDEA.

Endoparasitic Platyhelminthes without cilia and without digestive cavity, the animal consisting in most cases of a rounded head bearing organs of adhesion in the form of suckers and hooks, and an elongated compressed body consisting of a string of similar proglottides, each containing a complete set of hermaphrodite reproductive organs.

Sub-class I.—Cestodaria (Monozoa).

Body not divided into proglottides.

ORDER 1.—AMPHILINIDEA.

Mostly in the cœlome of Ganoid Fishes.
Example: *Amphilina.*

ORDER 2.—GYROCOTYLIDEA.

In the intestine of *Chimæra.*
Example: *Gyrocotyle* (Fig. 212).

Sub-class II.—Cestoda (Merozoa).

The body of the adult animal consisting of scolex and string of proglottides.

ORDER 1.—TETRAPHYLLIDEA.

Scolex with four usually stalked suckers. Larva in Copepods, adult in gut of Fishes, Amphibians and Reptiles.

ORDER 2.—DIPHYLLIDEA.

Scolex with two pairs of suckers, the members of each pair being fused; stalk of scolex armed with T-shaped spines; larva in Crustaceans and Molluscs; adult in gut of Elasmobranchs.

ORDER 3.—TETRARHYNCHIDEA.

Scolex with four suckers, each having a long, retractile proboscis beset with small hooks. Larva mostly in marine Invertebrates, adult in the gut of Elasmobranchs and Ganoids.
Example: *Tetrarhynchus* (Fig. 207).

ORDER 4.—PSEUDOPHYLLIDEA.

Scolex generally with two, sometimes without suckers. Hooks usually absent. The external divisions between the proglottides sometimes indistinct (*Ligula*). Larva in Crustaceans and Fishes, adult in fresh-water Fishes, Birds, and Mammals. In some forms (*Caryophyllæus* and *Archigetes*) the larva develops gonads pædogenetically and a segmented adult stage is absent. These forms have a certain resemblance to the monozoan Cestodes, *e.g.*, *Gyrocotyle* (Fig. 212).

Examples: *Dibothriocephalus* (Fig. 217), *Caryophyllæus* (Fig. 210), *Archigetes* (Fig. 211), *Ligula* (Fig. 209).

ORDER 5.—CYCLOPHYLLIDEA.

Scolex with four cup-shaped suckers and a rostellum armed with one or two rows of hooks. Larva in Crustaceans, Insects, or Vertebrates, adult in Vertebrates. The majority of the common Tapeworms belong to this order.

Example: *Tænia* (Figs. 193, 196, 208).

3. GENERAL ORGANIZATION.

General External Features.—As the name of the phylum denotes, the body in the Platyhelminthes is, in the great majority of cases, much compressed in the dorso-ventral direction; very thin, so that when very short it may be described as leaf-like, or, when more elongated, as ribbon-like; or thickish in the middle and becoming thinner towards the margin. Some, however, have the body comparatively thick, usually with a certain amount of dorsoventral compression; a few are approximately cylindrical or fusiform. The symmetry is always *bilateral*, the radial arrangement of parts so prevalent in the Cœlenterata and primarily, as we have seen, associated with a fixed or stalked condition, never being observable. A Flat-Worm has dorsal and ventral surfaces, right and left sides or borders, and anterior and posterior ends. The anterior end is that which is directed forwards in ordinary locomotion: it usually has some of the features which distinguish a head-end; but a distinct head is rarely developed, and the mouth, when present, is usually placed some distance back on the ventral surface.

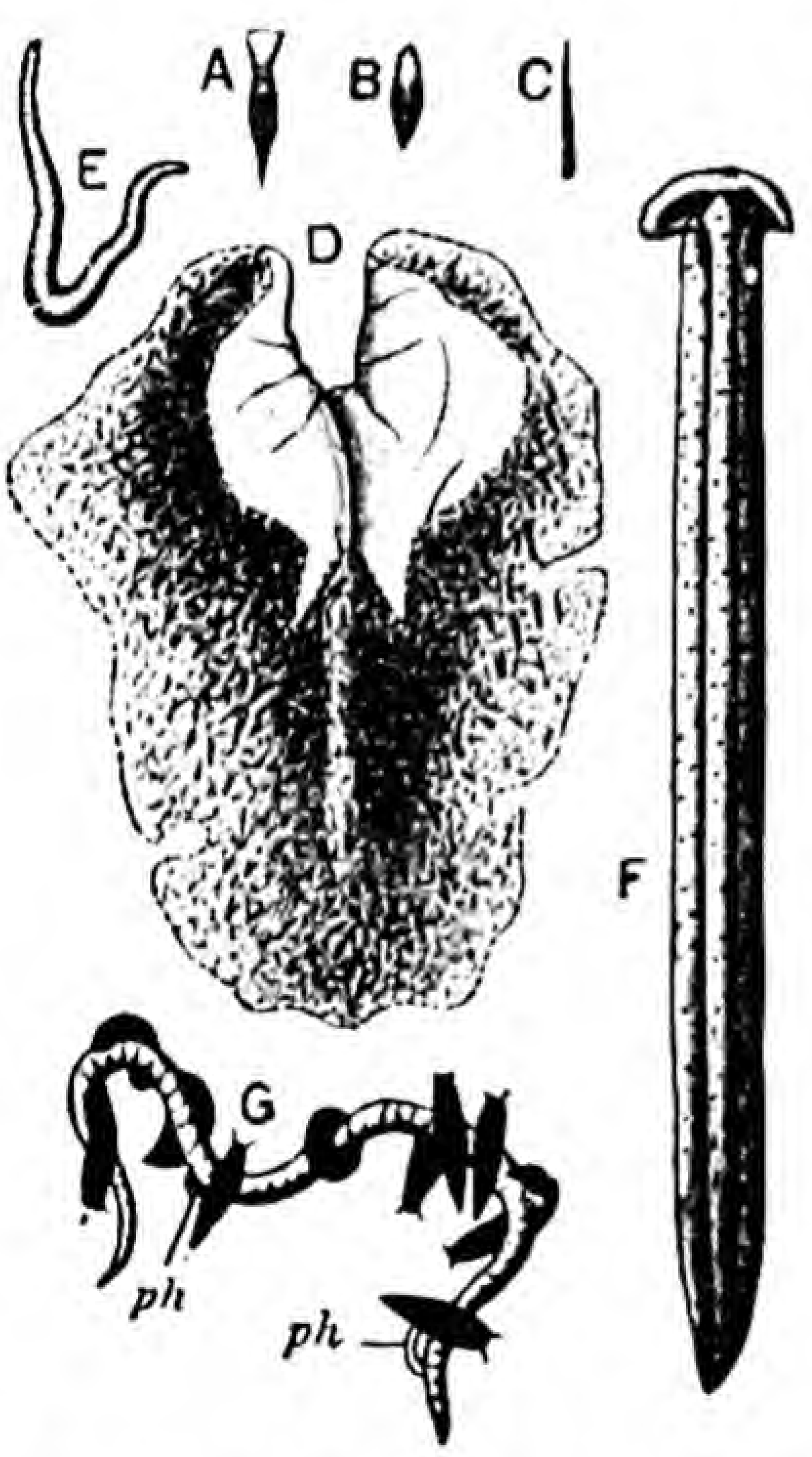


FIG. 199.—Various **Planarians.** *A*, Convoluta; *B*, Dalyellia (Vortex); *C*, Monotus; *D*, Thysanozoon; *E*, Rhynchodemus; *F*, Bipalium *G*, Polycelis. All natural size. (After Von Graff.)

In the *Turbellaria* (Fig. 199) the leaf-form is the prevailing one, a shape resembling that described for Planaria being very common. In many, however, the body is greatly elongated, and it may assume the shape of a thin ribbon with puckered edges, as in some marine forms; or may be thickened and band-like, as in the Land Planarians; or it may approach the shape of a cylinder, as in some Rhabdocœles. A head-region is not usually distinct;

but there is always something to mark off the anterior from the posterior end—a difference in shape, the presence of eyes, and, sometimes, of a pair of short tentacles; in some a slight constriction separates off an anterior lobe, on which the eyes are borne, from the rest of the body. In others the anterior end is retractile, and may be everted as a proboscis. The mouth is never at the extreme anterior end, but always ventrally placed, sometimes behind the

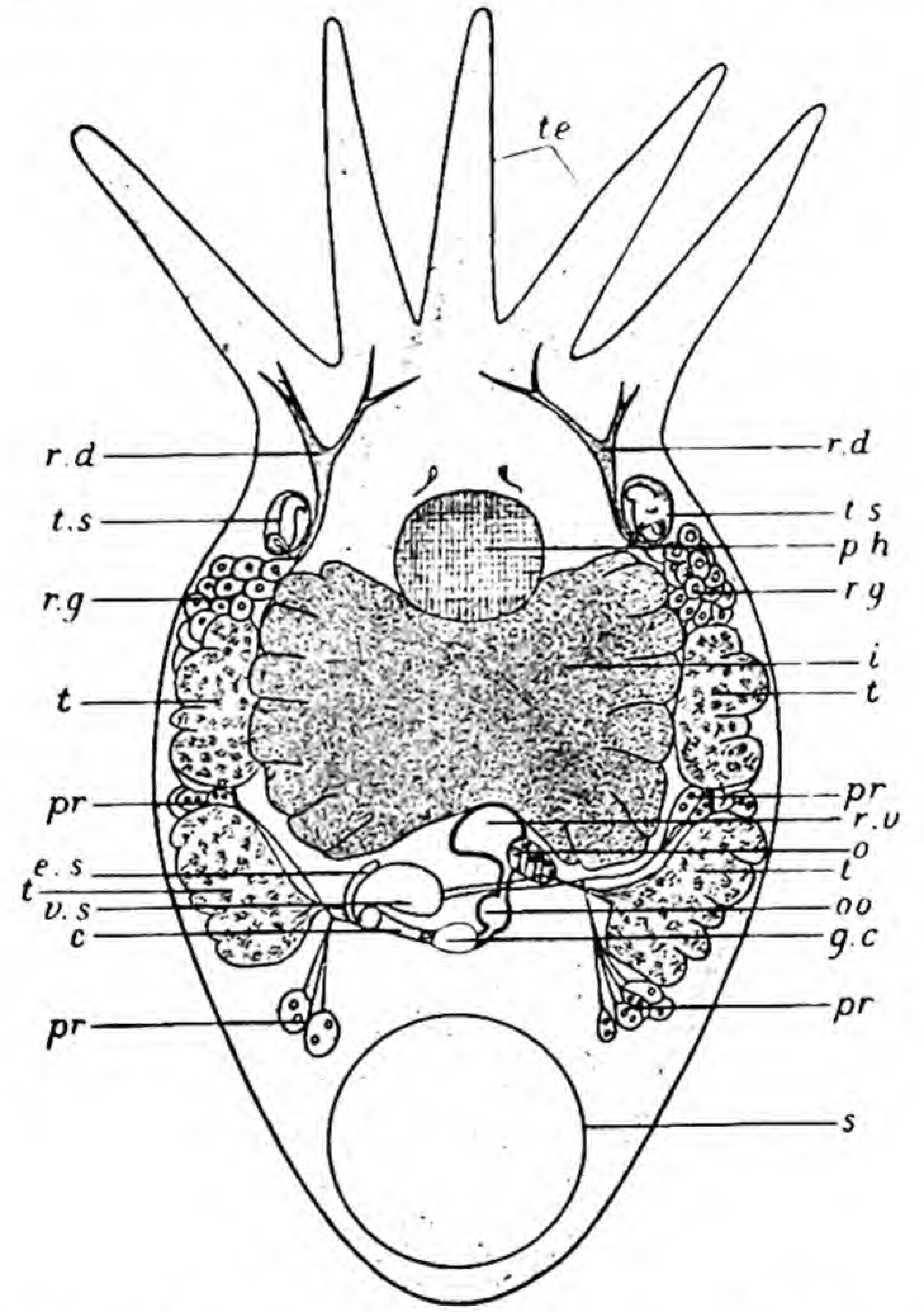


FIG. 200.—**Temnocephala minor,** general view of the organization. *c.* cirrus; *e. s.* ejaculatory sac; *g. c.* genital atrium; *i.* intestine; *o.* ovary; *oo.* ootype; *ph.* pharynx; *pr.* prostate glands; *r. d.* strands of ducts of integumentary glands running forwards to the tentacles; *r. g.* groups of integumentary (rhabdite-forming) glands; *r.v.* receptaculum; *s.* sucker; *t.* testes; *te.* tentacles; *t. s.* terminal sacs of excretory system; *v. s.* vesicula seminalis.

middle. In some Polycladida there is a small ventral sucker, probably with a copulatory function; and in some Rhabdocœles both the anterior and posterior ends, though not provided with suckers, are adhesive, so that the animal can loop along like a Hydra or a Caterpillar. In the *Temnocephalidæ* (Figs. 200 and 201) the anterior end develops a row of adhesive tentacles (only two in *Scutariella*); in *Actinodactylella* a series of marginal tentacles is

present in addition to anterior and posterior suckers. There is never any external appearance of segmentation, though in at least one exceptional instance (*Procerodes lobata*, Fig. 202) the internal parts may be so disposed as to approximate to the metameric arrangement (*pseudo-metamerism*). In such a case a number of transverse muscular septa are present, imperfectly dividing the body internally into a series of segments; and various internal

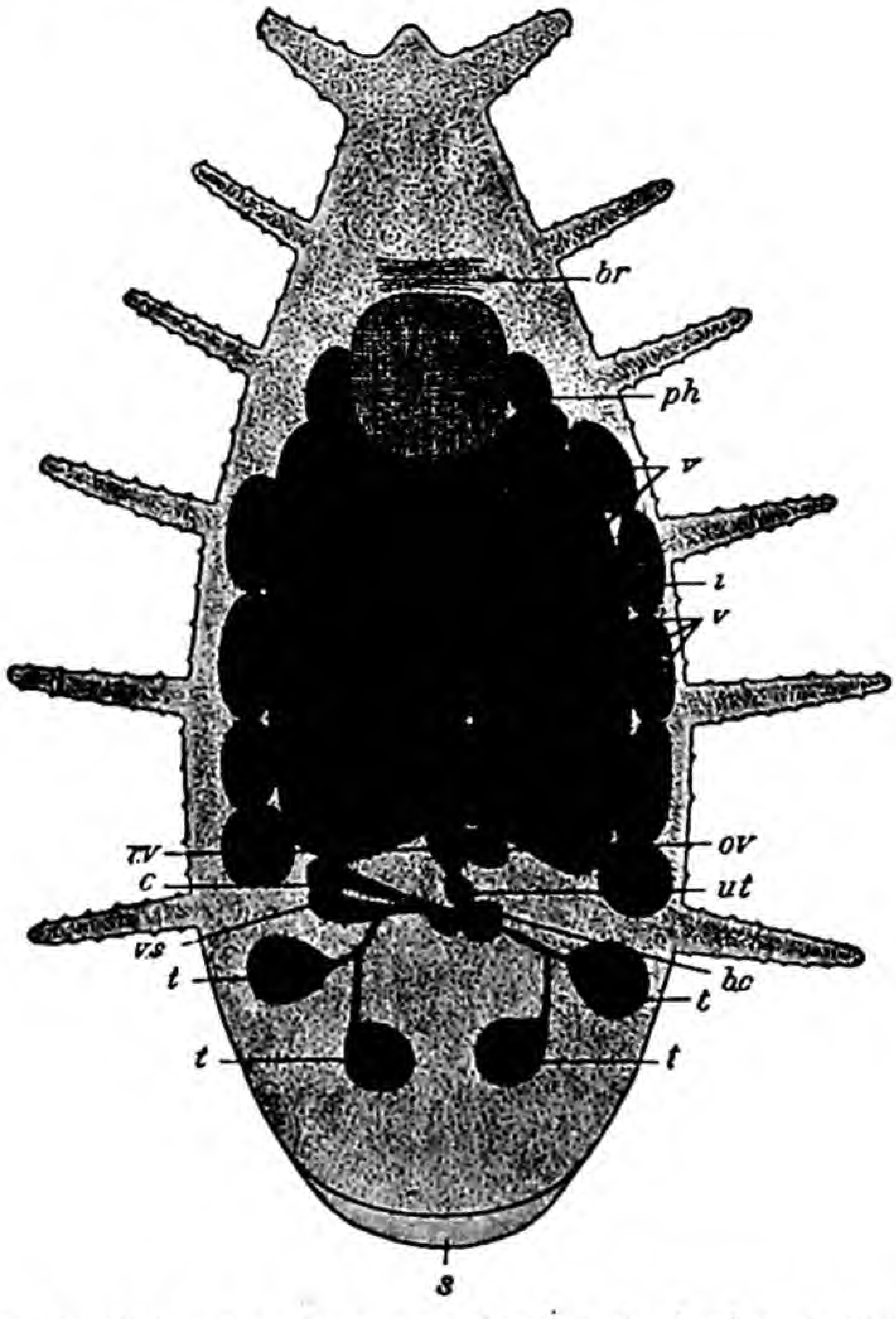


FIG. 201.—**Actinodactylella.** *b. c.* bursa copulatrix; *br.* brain; *c.* penis; *i.* intestine; *ov.* ovary; *ph.* pharynx; *r.v.* receptaculum; *s.* sucker; *t., t.* testes; *ut.* uterus; *v.* vitelline glands; *v. s.* vesicula seminalis.

organs—intestinal cæca, gonads, transverse commissures of the nervous system—are arranged in pairs following this division. A few Turbellaria multiply by *budding*, and these form long chains, having something in common with the string of proglottides of a Cestode, but differing radically, as will be shown later, in the mode of development. *Colour* is very general in the Turbellaria, though some are transparent and colourless. The most vivid coloration characterizes some of the marine Polyclads, the Rhabdocœles being

comparatively obscure. The surface is covered with a coating of fine *vibratile cilia*, the vibration of which subserves respiration as well as (in the smaller forms) locomotion. Among the ordinary cilia are frequently disposed longer whip-like cilia or flagella, likewise motile; and sometimes non-motile (sensory) cilia may occur here and there.

The *Trematodes* (Figs. 189, 203–206), nearly related to the Turbellarians in internal organization, resemble them also in external form, with certain modifications connected with a parasitic mode of life. As in the latter class, the leaf-shape prevails; an elongated form also occurs, though more rarely. The body is usually thicker and more solid than in most Turbellaria. The anterior end is distinguished from the posterior by its shape, by the arrangement of the suckers, and, in many of those Trematodes that are external parasites, by the presence of eyes. Suckers, present in the Turbellaria only in some of the Polycladida and a few Tricladida, are universal in their occurrence. They are always ventrally placed, their chief function being to fix the parasite to the surface of its host in such a way as to facilitate the taking in by the mouth of animal juices and epithelial débris; their number and arrangement vary considerably. There are nearly always present an anterior set of suckers (or a single anterior sucker surrounding the mouth) and a posterior set, or a single large posterior sucker. The arrangement already described as characterizing the

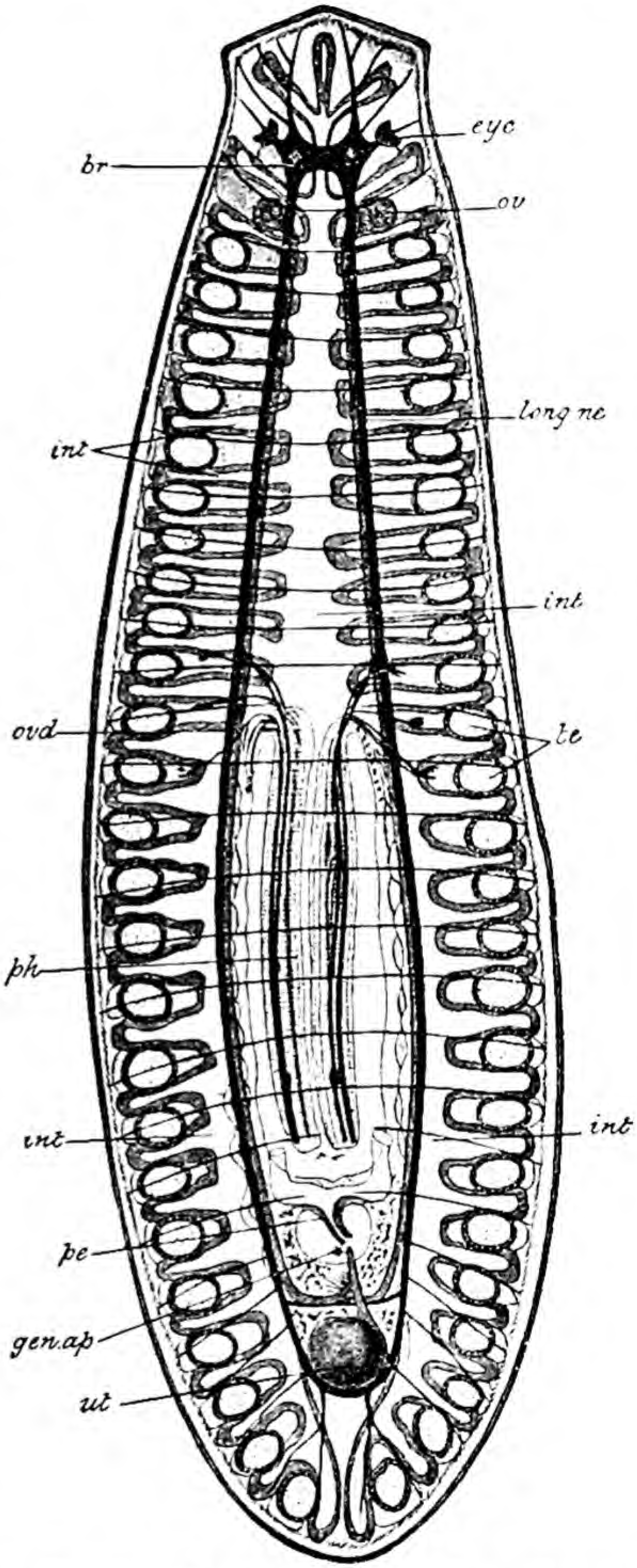


FIG. 202.—**Procerodes lobata.** General view of the organization. *br.* brain; *eye*, eye; *gen. ap.* genital aperture; *int.* intestine with its cæca; *long. ne.* longitudinal nerve-cord; *ov.* ovary; *ovd.* oviduct; *pe.* penis; *ph.* pharynx; *te.* testes; *ut.* uterus. (After Lang.)

Liver-Fluke is that which is typical in the digenetic forms—a single anterior and a single posterior sucker; but in some of the *Digena* the posterior sucker

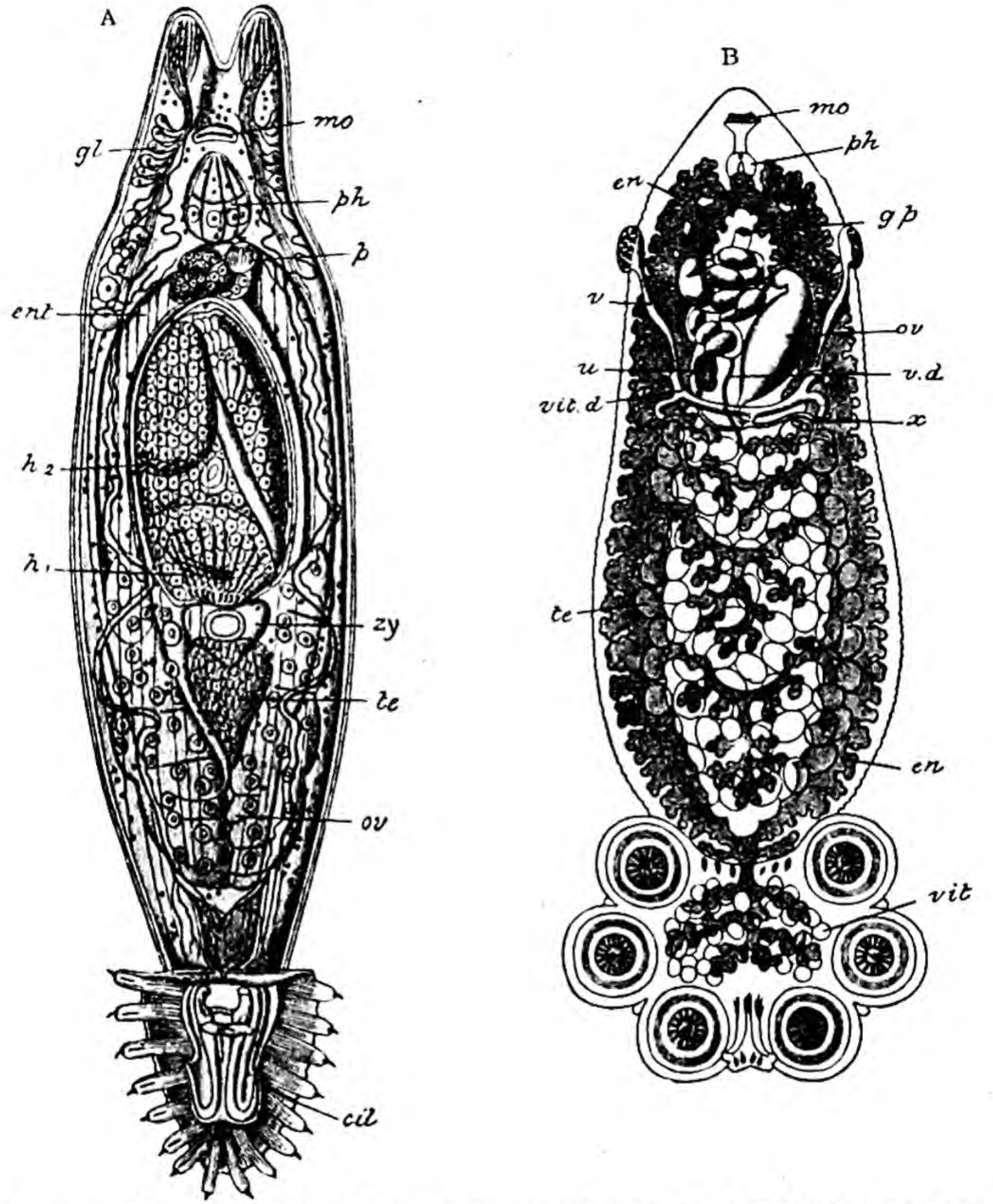


FIG. 203.—**Monogenetic Trematodes.**—*A*, *Gyrodactylus*. *cil.* disc bearing hooks and processes at the posterior end; *ent.* intestine; *gl.* unicellular glands whose ducts open on the surface about the anterior end; h_1. caudal disc of the first embryo; h_2. caudal disc of the second embryo; *mo.* mouth; *ov.* ovary; *p.* penis; *ph.* pharynx; *te.* testes. *B*, *Polystomum*, *en.* intestine; *g. p.* genital pore; *mo.* mouth; *ph.* pharynx; *ov.* ovary; *te.* testes; *u.* uterus; *v.*, *v. d.* vas deferens; *vit.* vitelline glands; *vit. d.* vitelline ducts; *zy.* fertilized ovum; *x* marks the position of the genito-intestinal canal connecting the oviduct with the intestine. (From M. Braun.)

is wanting. Adhesive papillæ on the dorsal or ventral surface may supplement the adhesive action of the suckers (Fig. 206). In the Monogena the suckers are often more numerous; in the family *Gyrodactylidæ* (Fig. 203, *A*) there

is no anterior sucker, but at the posterior end one or two discs armed with hooks; in the *Polystomeæ* (Fig. 203, *B*) there is also a posterior disc on which are six suckers with several hooks. In the *Aspidobothridæ* there is only a single sucker; but it extends over nearly the whole of the ventral surface, and is complicated in structure owing to its cavity being divided into a number of compartments by a system of partitions.

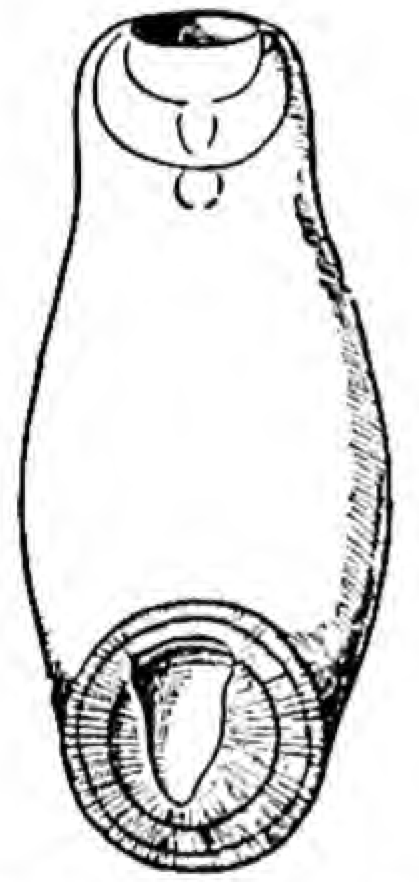


FIG. 204. — **Amphistomum sp.** From the gut of Chelone. (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co.), original Fuhrmann.)

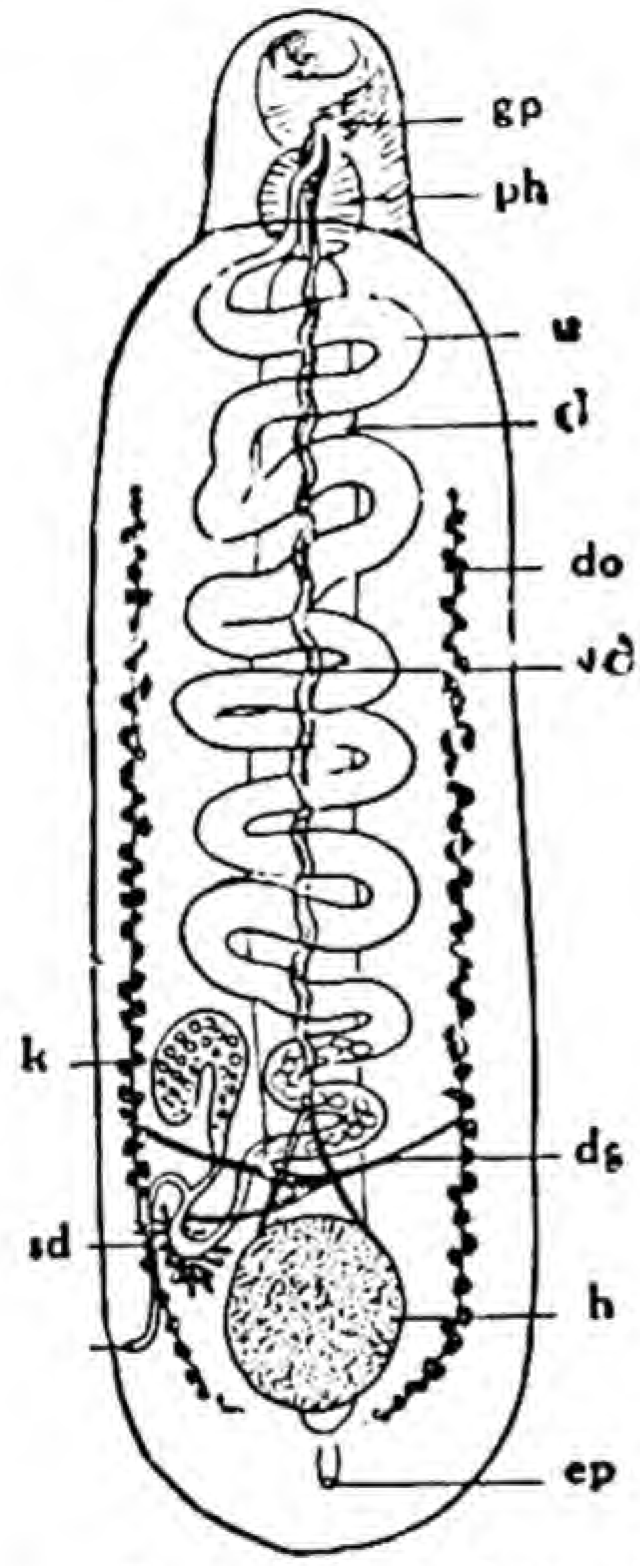


FIG. 205.—**Lophotaspis vallei Stossich.** From the gut of Thalassochelis. *d.* cylindrical gut; *d. g.* vitelline duct; *do.* vitelline glands; *e. p.* excretory porus; *g. p.* genital porus; *h.* testis with two vasa efferentia; *k.* ovary; *ph.* pharynx; *s. d.* shell gland; *u.* uterus; *v. d.* vas deferens. (From Fuhrmann, after Looss.)

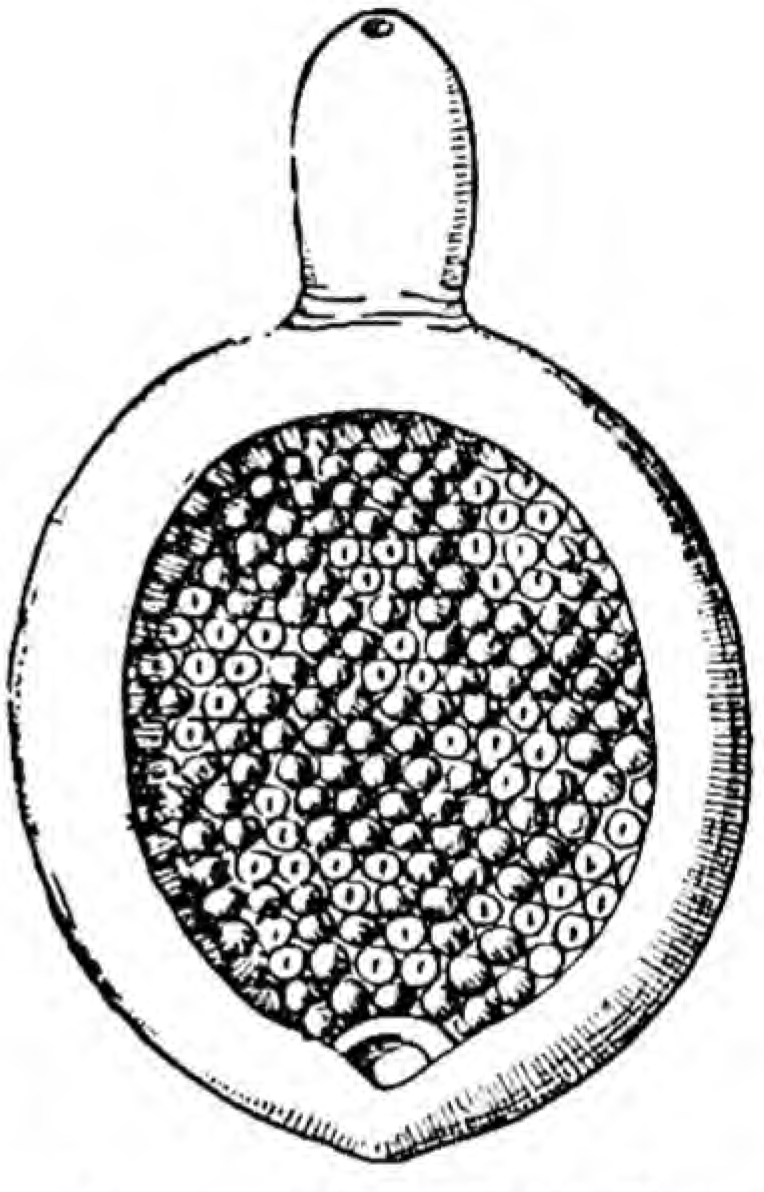


FIG. 206. — **Gastrodiscus ægypticus Cobbold.** From the gut of the Horse. (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co.), original Fuhrmann.)

Vibratile cilia are not known to occur on the surface in the adult condition; in some there are groups of non-motile cilia, situated on little conical elevations—the *tactile cones.* Pigment is rare in the endoparasitic Digena, save in a few that live in the interior of transparent animals; though many appear coloured variously by the internal organs shining through the translucent body-wall, or are stained by some fluid derived from their host. Pigment occurs in some of the ectoparasitic forms.

The relationship of the *Cestoda* to the Trematoda is, as will be subsequently shown, fairly close; but though there are connecting forms between the two classes, the shape of the average Cestode is very different from that of an

Fig. 207.—**Tetrarhynchus.** *n.* nervous system; *r.* proboscides; *rs.* sheaths, with their muscles (*rb.*). (From Leuckart, after Pintner.)

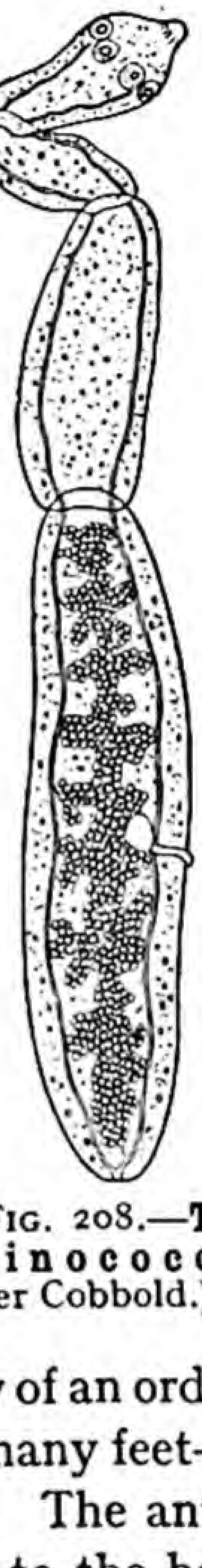


Fig. 208.—**Tænia echinococcus.** (After Cobbold.)

average Trematode such as the Liver-Fluke. The body of an ordinary Cestode is of great length—sometimes extending even to a good many feet—and relatively narrow, being compressed into the form of a ribbon. The anterior end is, in most cases, attached to the host by means of suckers and hooks placed on a rounded lobe, the *head* or *scolex*, connected with the body by a narrow part or *neck*. The head is usually rather radially than bilaterally symmetrical, with four suckers and a circlet of hooks. The hooks, when present, are borne on a longer or shorter retractile process, the *rostellum*, the long axis of which is in line with the long axis of the body. In *Dibothriocephalus* and allied forms (Pseudophyllidea) a pair of longitudinal grooves take the place of suckers, and there are no hooks. In many Cestodes parasitic in Fishes the head bears four prominent, thin, folded flaps—the *bothridia*, which

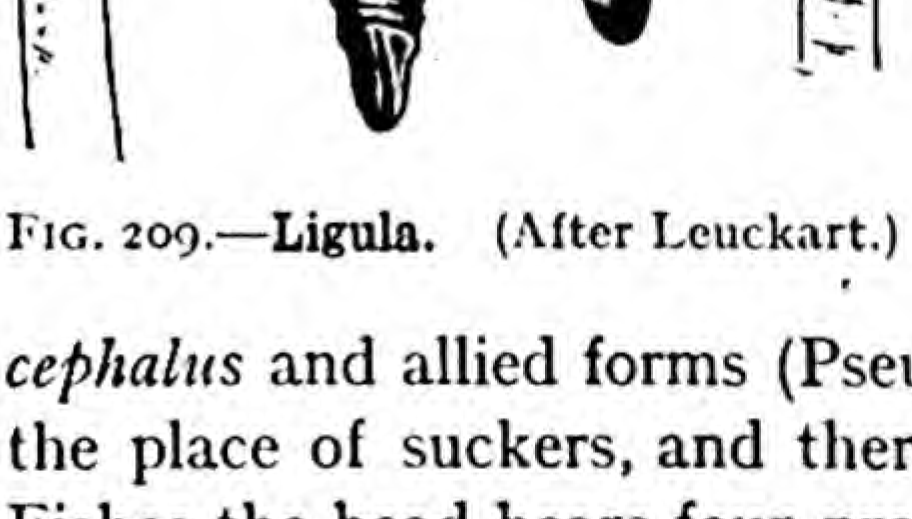


Fig. 209.—**Ligula.** (After Leuckart.)

are exceedingly mobile, and are used more as creeping organs than as organs of fixation. In relation to each of these bothridia, which, by coalescence, may appear to be reduced to two, may be a small sucker of the ordinary kind. In *Tetrarhynchus* (Fig. 207) there are four very long and narrow rostella, or "proboscides," covered with hooklets, and capable of being retracted into sheaths.

The Cestoda are devoid of mouth, and in most of them the genital apertures are marginally placed, so that, externally, there is—except in the case of a few in which the genital apertures are not marginal—nothing to distinguish the dorsal surface from the ventral. The *body*, or *strobila*, which is narrower in front than it is further back, is made up throughout its length of a series of segments, or *proglottides*, which become larger and more distinctly marked off from one another as we pass backwards. *Tænia echinococcus* (Fig. 208) is exceptional in possessing only three or four proglottides. In some of the Pseudophyllidea (*Ligula*, Fig. 209) though the body has the normal elongated ribbon-like form, the segments are not distinct. *Caryophyllæus* (Fig. 210) and *Archigetes* (Fig. 211) belonging to the same order are unsegmented larval forms, a segmented adult stage being absent. In the Cestodaria *Amphilina* and *Gyrocotyle* (Fig. 212) segmentation is entirely absent, the whole body in these genera consisting of a single proglottis. The surface in the Cestodes is devoid of cilia, and there is no pigment.

Integument and Muscular Layers.—In the Platyhelminthes in general there are *integumentary* layers and underlying layers of *muscle*, which are more highly differentiated than in the Cœlenterates. But considerable differences exist in this respect between the members of the three classes. These have already been dealt with in the account of the examples of the phylum.

Characteristic of the Flat-Worms is a peculiar form of connective tissue, the **parenchyma**—presenting many varieties, filling up the interstices between the organs and leaving only, in some instances, very small spaces—sometimes regarded as representing the body-cavity, which we shall meet with in other groups of worms. Sometimes the parenchyma appears to consist of distinct large cells with greatly vacuolated protoplasm, with interspaces here and there in which groups of rounded cells are enclosed. Sometimes the constituent cells run together, and the parenchyma then appears as a nucleated, finely fibrillated, vacuolated mass in which the boundaries of the cells are not recognizable. Pigment occurs in the parenchyma in some rhabdocœle Turbellarians and a few monogenetic Trematodes. In some Turbellaria—species of *Convoluta* and *Dalyellia* (*Vortex*)—the parenchyma contains numerous cells enclosing chlorophyll or xanthophyll bodies; these are symbiotic unicellular Algæ, similar in their mode of occurrence to the yellow cells which have been referred to as found in the Radiolaria. Running through the body, for the most part in a dorso-ventral direction, are numerous

slender muscular fibres, the fibres of the *parenchyma muscle*; many of these become inserted externally into the basement membrane.

Great differences exist between the various groups of Platyhelminthes as regards the development of the **alimentary system,** differences which are, broadly, to be correlated with differences in the mode of nutrition. Some of

FIG. 210.—**Caryophyllæus.** *d. g.* vitelline duct; *d. st.* vitelline glands; *e.* excretory pore; *k.* mobile organ; *od.* oviduct; *ov.* germarium; *p.* cirrus; *r. s.* receptaculum seminis; *t.* lobes of testes; *v. d.* vas deferens; *v. s.* vesicula seminalis; *w.g.o.* female aperture. (After Leuckart.)

FIG. 211. —**Archigetes.** (After Leuckart.)

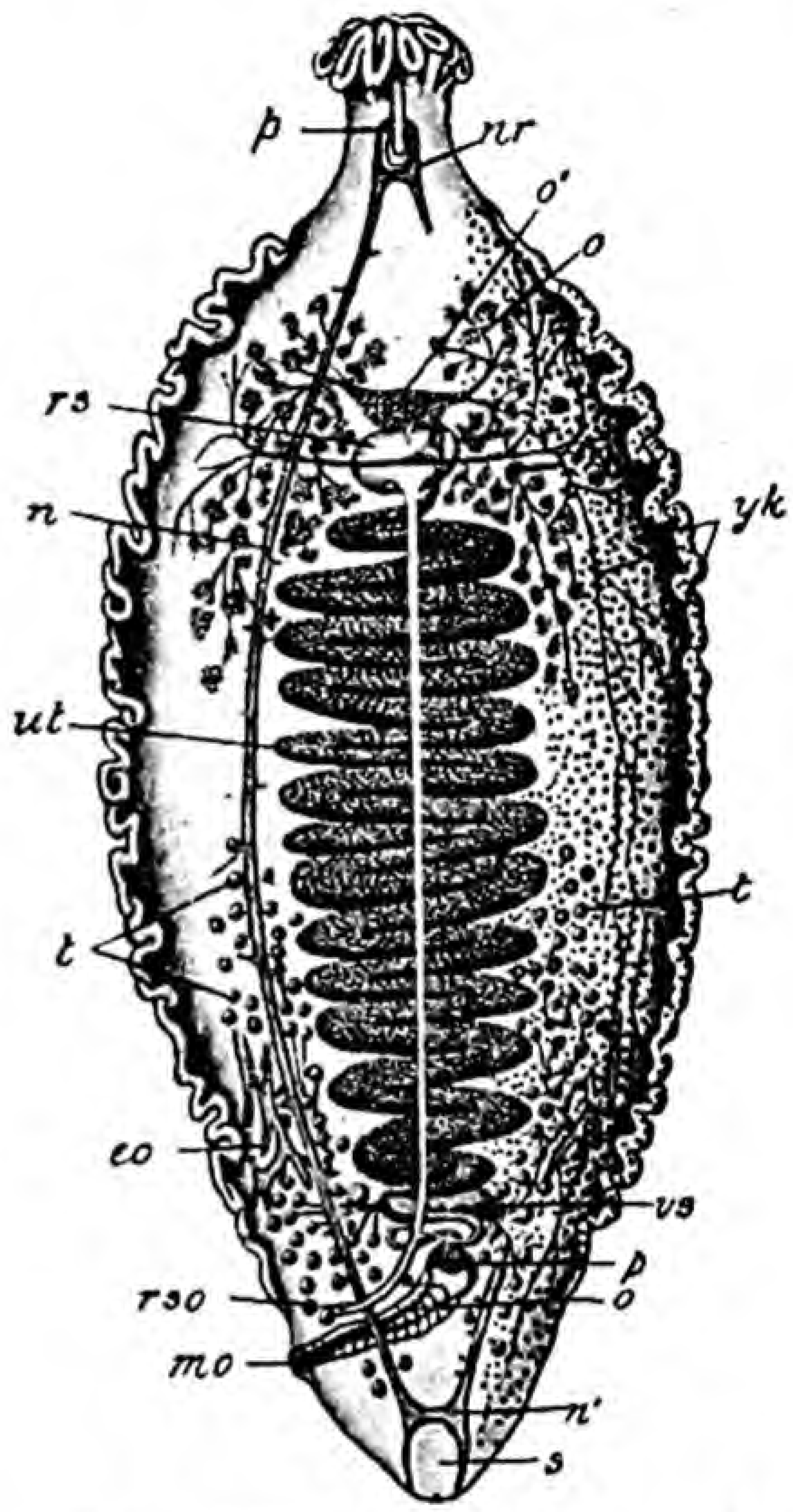


FIG. 212.—**Gyrocotyle (Amphiptyches).** *eo.* excretory opening; *mo.* male opening; *n.* longitudinal nerve; *n'.* anterior nerve-ring; *n.r.* posterior nerve-ring; *o.* opening of uterus; *o.* ovary; *o'.* receptaculum ovorum; *p.* base of cirrus; *r. s.* receptaculum seminis; *r. s. o.* opening of vagina; *s.* sucker; *t.* testes; *ut.* uterus; *v. s.* vesicula seminalis; *yk.* vitelline glands. (After Spencer.)

the Flat-Worms—the Turbellaria and some of the monogenetic Trematodes—procure their food, in the shape of small living animal or vegetable organisms, or floating organic débris, by their own active efforts. Others—the digenetic Trematodes and the Cestodes—having reached a favourable situation in the interior of their host, remain relatively or completely passive. An alimentary canal is completely absent in the last-named group, nutrition being effected

by the absorption of digested matter from the interior of the animal in which the Cestode lives. In all the rest of the Platyhelminthes there is an alimentary canal, which very rarely opens on the exterior by an anal aperture. All the Turbellaria (except some *Acœla*) and Trematoda have an alimentary apparatus

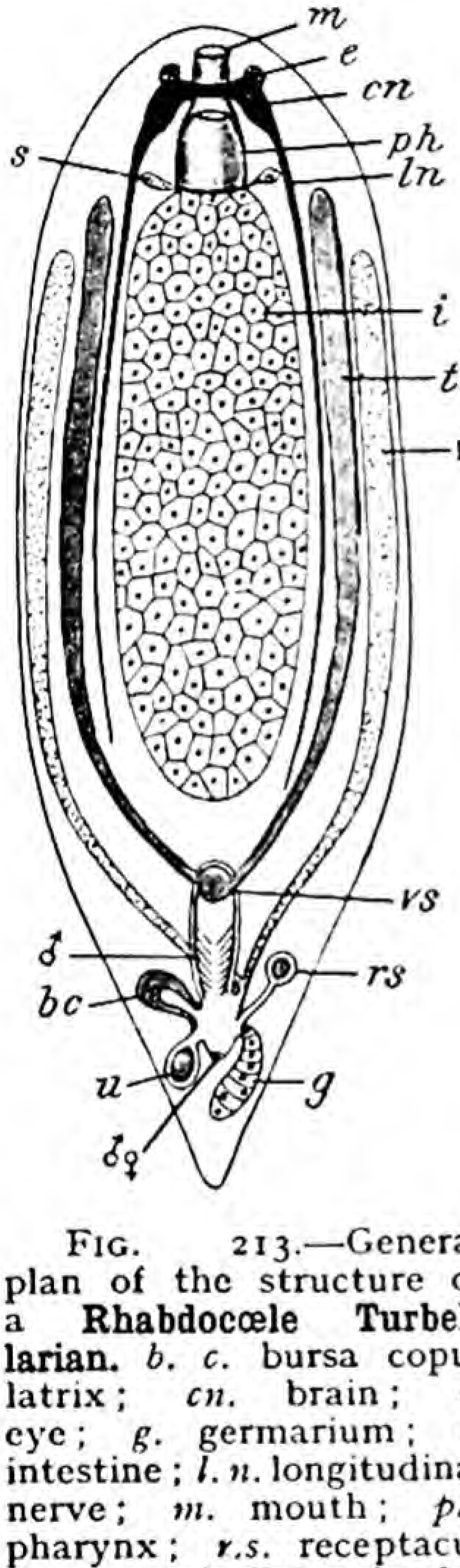


FIG. 213.—General plan of the structure of a **Rhabdocœle Turbellarian.** *b. c.* bursa copulatrix; *cn.* brain; *e.* eye; *g.* germarium; *i.* intestine; *l. n.* longitudinal nerve; *m.* mouth; *ph.* pharynx; *r.s.* receptaculum; *s.* unicellular glands; *t.* testis; *u.* uterus; *v.* vitellarium; *v. s.* vesicula seminalis; ♂ ejaculatory duct; ♂ ♀ common genital aperture. (After Von Graff.)

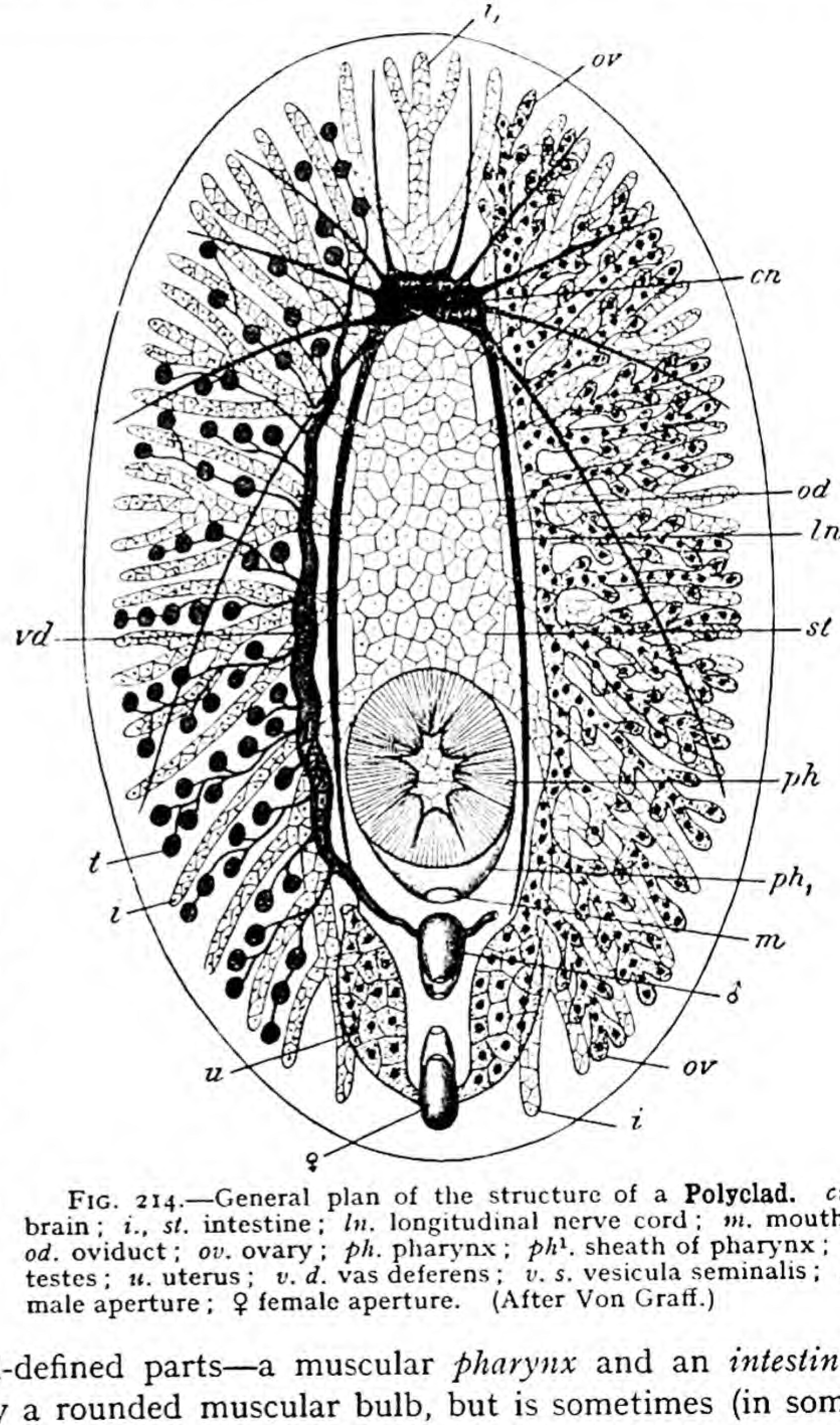


FIG. 214.—General plan of the structure of a **Polyclad.** *cn.* brain; *i.*, *st.* intestine; *ln.* longitudinal nerve cord; *m.* mouth; *od.* oviduct; *ov.* ovary; *ph.* pharynx; *ph*[1]. sheath of pharynx; *t.* testes; *u.* uterus; *v. d.* vas deferens; *v. s.* vesicula seminalis; ♂ male aperture; ♀ female aperture. (After Von Graff.)

consisting of two well-defined parts—a muscular *pharynx* and an *intestine*. The pharynx is usually a rounded muscular bulb, but is sometimes (in some Turbellaria) of a cylindrical shape; it is usually capable of eversion and retraction. *Actinodactylella* (Fig. 201) is exceptional in having, in addition to a large muscular pharynx, an extensile proboscis with a pin-shaped style,

which becomes retracted within the opening of the mouth. Unicellular glands open into the pharynx in most cases.

The *mouth* is always ventral, but varies greatly in its position on the ventral surface, being sometimes central, sometimes situated behind, sometimes in front of, the middle of the length of the body. In the most lowly organized group of Turbellaria, the *Acœla*, the *intestine* is represented merely by a vacuolated, nucleated mass of syncytial parenchyma-tissue. In the others the intestine is sometimes a simple sac (rhabdocœle Turbellaria (Fig. 213,) and a few Trematoda), with or without short lateral diverticula. In the majority of the Trematodes it consists of a pair of simple canals; but in some, as in the Liver-Fluke, there is a pair of canals which give off numerous branches. In the Polycladida (Fig. 214) there is a central cavity from which numerous branching canals are given off. In the Tricladida (Fig. 215) one median canal passes forwards from the pharynx, and a pair of canals backwards from it, all three giving off branches which again branch. In some Polycladida there are minute pores, by means of which certain of the canals are placed in communication with the exterior. A number of unicellular glands, which probably produce a digestive secretion, open in many Trematodes and Rhabdocœles at the junction of pharynx and intestine.

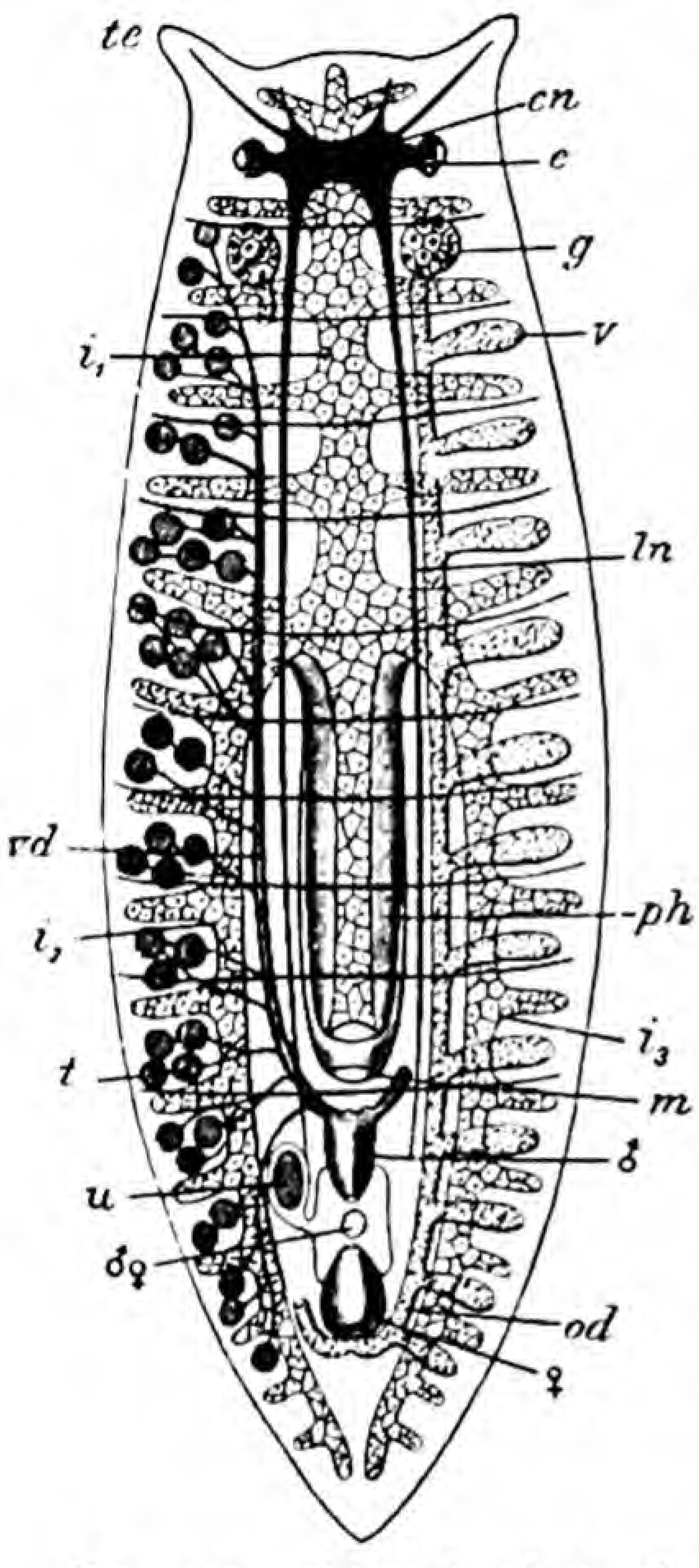


FIG. 215.—General plan of the structure of a **Triclad.** *cn.* brain; *c.* eye; *g.* germarium; i_1. median limb of the intestine; i_2. right limb; i_3. left limb; *l. n.* longitudinal nerve-cord; *m.* mouth; *od.* oviduct; *ph.* pharynx; *t.* testes; *te.* tentacles; *v.* vitellaria; *v. d.* vas deferens; *u.* uterus; ♂ ejaculatory duct; ♀ vagina; ♂ ♀ common genital aperture. (After Von Graff.)

A bilateral **nervous system** is developed in all the Platyhelminthes. Its elements are *nerve-fibres* and *nerve-cells*. The nerve-cells, which are usually bipolar, more rarely uni- or multi-polar, lie in the course of these fibres, with which the substance of the cells is in continuity. The degree of development of a central part of the nervous system, or *brain*, varies in the different groups; it is best developed in some Polycladida and some monogenetic Trematodes. It consists of numerous nerve-fibres which here converge from the various parts of the body and pass across from one side to the other, together with a central mass of fine fibrils, and a number of nerve-cells. It is situated in the anterior portion of the body, almost invariably in front of the mouth. Where the peripheral part

of the nervous system is best developed, as it is in the Polycladida, the Tricladida, and some Trematodes, there are three pairs of longitudinal *nerve-cords* running backwards from the brain throughout the body, connected together by frequent transverse connecting nerves, or *commissures*. To these there are sometimes super-added fine networks or *plexuses* of nerves, situated superficially under the dorsal integument, or on both dorsal and ventral surfaces. Sometimes nerves run forwards from the brain as well as backwards. In the Rhabdocœles and some of the Trematodes the whole system is simpler, and the number of longitudinal cords fewer. In the Cestodes there are two principal longitudinal trunks which run throughout the length of the body, and are connected together in the head by commissures, variously thickened to form ganglia representing the brain of other Platyhelminthes.

In addition to the *tactile cones* of some Trematodes and the *sensory cilia* and *auricular organs* of the Turbellaria, already referred to, the chief **sense-organs** of the Platyhelminthes are the eyes and the statocysts. *Eyes* occur in the Turbellaria and some monogenetic Trematodes, but are wanting in the digenetic Trematodes and in the Cestodes. In some of the Polycladida they are extremely numerous, collected into groups over the brain, and frequently arranged also round the margin of the body. In the Rhabdocœles and monogenetic Trematodes they are much less numerous—usually two to four. In some cases each eye simply consists of a pigment spot; to this may be added a refractive body. When most highly developed the eye (Fig. 187) is still of very simple structure, consisting of a cup formed of one or more pigment-cells having sensory cells in close relation to it with processes (nerve-fibres) passing to the brain. The *statocysts* are sacs containing *statoliths* of carbonate of lime. Occurring only in a small number of the Turbellaria, they are *gravity receptors* concerned with the control of the *geotactic behaviour* of the animals. *Ciliated pits* which are modified auricular organs are developed in the head region of some Rhabdocœles.

The only **vascular system** present in the Platyhelminthes is the system of *water-vessels* (*protonephridia*) which are commonly regarded as performing an osmoregulatory and excretory function. This system of water-vessels opens on the exterior in a variety of different ways: sometimes it opens by a number of minute pores; sometimes, as in the Liver-Fluke, there is a single posterior aperture; frequently there are two. In the Tricladida there are two longitudinal canals which open on the exterior through special branches by a series of pores. In the Rhabdocœla there are either two longitudinal main vessels or a single median one; the communication with the exterior in the former case may be by a pair of ventral apertures, or indirectly through the pharynx; or there may be a common short passage in which the two trunks unite, opening by a posterior median aperture. When a single main trunk is present it

opens at the posterior end of the body. In the Trematodes there are usually two principal longitudinal trunks, which either unite behind to open at the posterior end of the body, or (Monogena) remain separate and open independently on the dorsal surface, each having, where it opens, a contractile *excretory sac*.

In the Cestodes there are usually four longitudinal trunks, which open through a contractile excretory sac at the posterior end of the body. In many cases it has been shown that the main trunks communicate with the exterior at intervals by means of fine canals. The excretory sac is thrown off when the last proglottis becomes separated off and does not in most cases become renewed, though in at least one species of Tape-worm (*Tænia cucumerina*) a new vesicle is developed again and again at the end of the body as a fresh segment is thrown off. The main trunks are connected together by a *ring-vessel* in the head and in some cases by a *transverse branch* in each proglottis, and where the latter originate from the main trunks are valves formed by folds of the wall of the vessel. In the posterior region only two of the longitudinal trunks (one on each side) may be retained.

The sexes are united in all the Platyhelminthes with a few exceptions, and the **reproductive organs** are sometimes somewhat complicated—presenting a remarkable advance on those of the Cœlenterata.

In the *Acœla* there are in nearly all cases separate male and female apertures. The two testes are divided into numerous small lobes. There are no vitellaria in most cases—the two ovaries producing large ova containing abundant food-yolk and the substance of the egg-shell being formed from droplets in the latter. Oviducts are absent in most cases. Into the main female genital passage or *antrum femininum* opens a peculiar single or double sac or *bursa*, usually provided with chitinous structures. In one case at least (*Heterochærus*) there is a passage leading from the antrum femininum to an aperture on the dorsal surface.

In the Rhabdocœles (Figs. 213 and 216) there are usually only two compact testes and two vasa deferentia leading to the unpaired male aperture at the extremity of the cirrus. The *prostate* or *granule glands*—a set of unicellular glands, which secrete round, bright granules destined to mix with the sperms—are specially well developed in the Rhabdocœles, and are present in some other Turbellaria and in certain Trematodes. Ovaries (germ-vitellaria) alone occur in some, separate germaria and vitellaria in others; there are either two germaria or one only. A *receptaculum* may be present as a swelling or diverticulum of the main female duct, or of the atrium. The terminal part of this duct may form a muscular *vagina*, or there may be a muscular *bursa copulatrix* developed from the wall of the atrium. A *uterus* is present in most cases as an outgrowth from the wall of the atrium. Male and female ducts have a common chamber or *genital atrium* with a single external opening.

In the *Temnocephalidæ* (Figs. 200, 201) there are a genital atrium and a single genital aperture. There are two pairs of compact testes; the right and left vasa deferentia unite in a vesicula seminalis, and granule or prostate glands are well developed. The cirrus has a chitinous tube and a variety of eversible spines. There is a single compact germarium; the oviduct has connected with it a large receptaculum, and dilates posteriorly to form an ootype into which the "shell-glands" open. *Actinodactylella* alone has a *bursa copulatrix* (Fig. 201, *b. c.*).

In the Tricladida (Fig. 215) there are also numerous testes, but the fine tubes connecting them with the two *vasa deferentia* are absent. There are two germaria, situated far forwards, and numerous yolk-glands. Two oviducts, into which the yolk is discharged from the yolk-glands by a series of lateral apertures, lead from the ovaries to unite in a median *ootype* or *vagina*, receiving the ducts of glands which may secrete the substance of the cocoon. The condition is thus intermediate between that observable in most of the Rhabdocœles and that which characterizes the Polyclads. Though germaria and vitellaria are separate, they have a common duct, and might be regarded as distinct lobes of one germo-vitellarium. A uterus is present, formed as an outgrowth of the vagina or of the atrium, or as an independent sac or pair of sacs opening independently on the exterior. There may be a receptaculum seminis, and in some there is a duct of communication between this and the intestine (genito-intestinal canal). A common genital atrium with a single external aperture receives the ducts of both sexes.

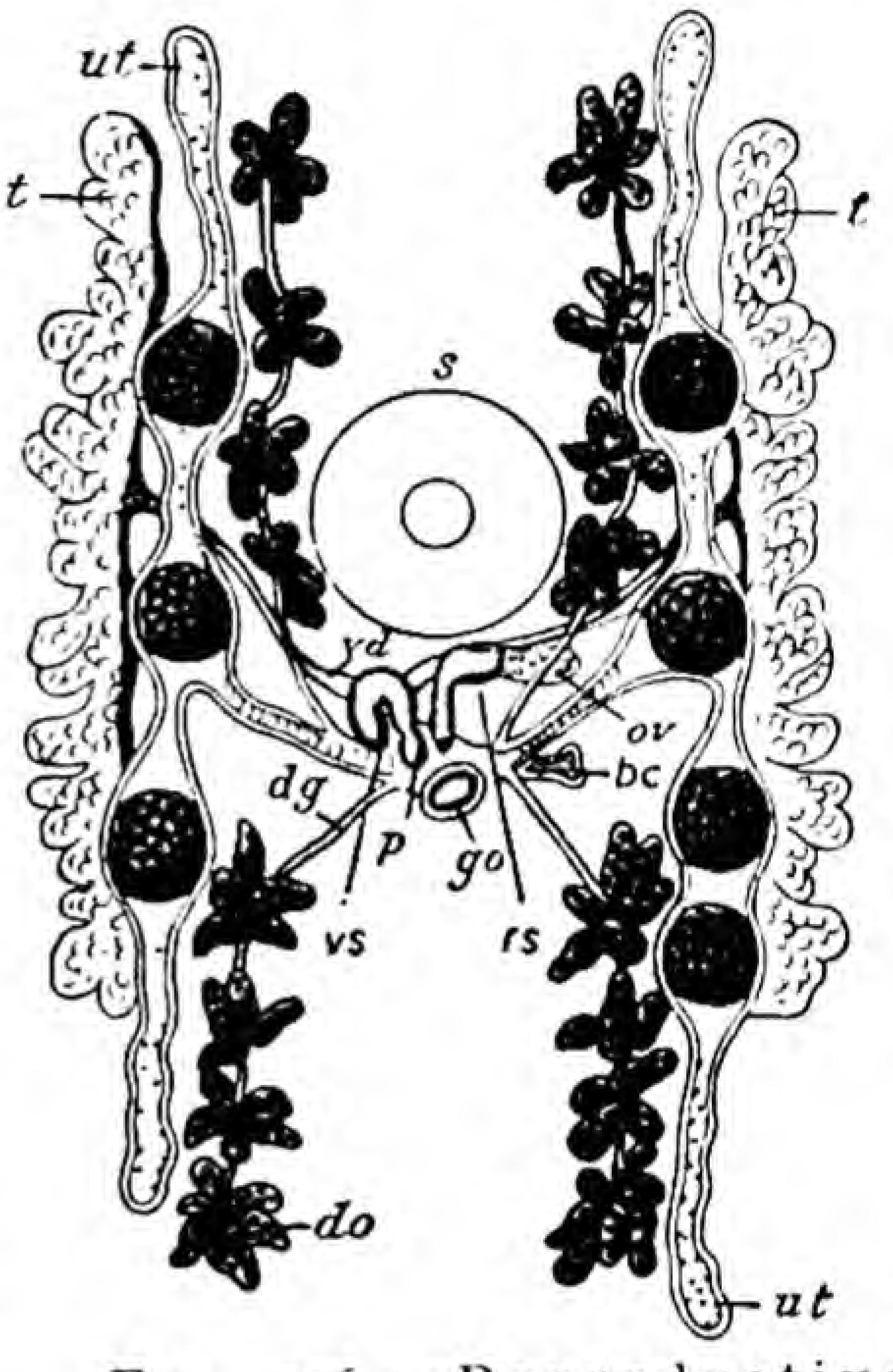


FIG. 216.—Reproductive organs of **Mesostoma ehrenbergii.** *b. c.* bursa copulatrix; *dg.* duct of vitelline glands; *do.* vitelline glands; *go.* common reproductive aperture; *ov.* ovary; *p.* cirrus; *r. s.* receptaculum seminis; *s.* pharynx; *t.*, *t.* testes; *ut.* uterus; *v. d.* vas deferens; *v. s.* vesicula seminalis. (From Claus, after von Graff and Schneider.)

In the Polyclad Turbellaria (Fig. 214) the *testes* are numerous, and there are a corresponding number of fine tubes which combine to form the two *vasa deferentia*, leading to the male aperture with its penis. The latter is sometimes double or multiple. The *ovaries* consist of numerous small rounded masses of cells, and there are no separate yolk-glands. Numerous narrow oviducts lead from the ovaries, and unite to form larger ducts; these, in turn, open into two elongated *uteri*, in which numerous large eggs containing abundant yolk collect. The ducts of the uteri open into a median *egg-duct* or *vagina*, with which the ducts of the accessory glands communicate, and in

which the eggs receive their chitinoid investment, derived in this case from the yolk-material of the substance of the ova. The vagina leads to the female aperture, a part of it being, in some cases, surrounded by a muscular sheath.

In many cases the egg-duct gives off posteriorly a narrow duct which usually terminates behind in a vesicle known as the *accessory sac* or *receptaculum*: this may be double. In a few Polyclads this duct opens on the exterior on the ventral surface some distance behind the main female aperture, in one instance on the dorsal surface. A *genito-intestinal canal* connecting this duct with one of the intestinal cæca has been found in one Polyclad. In most cases male and female apertures are distinct from one another, the former being situated in front of the latter. But sometimes, though rarely, both lead into a common chamber or *atrium* with a single opening on the exterior.

Most of the Trematodes have two testes (reduced to one in the Monogena and the Aspidogastridæ among the Digena), usually compact, sometimes branched; in a few instances there are four. The vasa deferentia unite into a median duct, which is dilated at the base of the cirrus to form a vesicula seminalis. There is a single oval or branched *germarium*, and two sets of vitelline glands. A canal termed *Laurer's canal* in some digenetic Trematodes, such as some species of *Fasciola*, leads from the exterior to the oviduct or vitelline duct. This may be replaced by a receptaculum seminis, or both structures may co-exist. The distal part of the oviduct is enlarged to act as a uterus. In the Monogena there is a vagina, which is sometimes paired, opening on the surface independently of the uterus: internally it communicates with the oviduct through the main vitelline duct. In some of the Monogena there is a genito-intestinal canal occupying a corresponding position to Laurer's canal, but opening into the intestine. In the Aspidogastridæ this is replaced by a stalked *yolk-receptacle*. There is nearly always a genital atrium common to the ducts of both sexes.

In the ordinary Cestodes each segment or proglottis contains a set of reproductive organs similar to those of a Trematode. There may be a single genital aperture leading into a genital atrium, into which both male and female ducts open; or the male and female apertures may be distinct. The testis is divided into numerous minute lobes, from which proceed a number of fine canals joining together to form the vas deferens, at the extremity of which is the chitinous cirrus. There are two germaria, and either a single vitelline gland, or two. The oviduct has its origin in a sort of isthmus connecting the two germaria. It receives a narrow fertilizing duct from the receptaculum seminis, and then the vitelline ducts, and becomes surrounded by a rounded mass of accessory glands to form the ootype, which is not definitely enlarged. Further forward it gives off the uterus. The latter is at first a simple cylindrical outgrowth from the oviduct, but it usually becomes large and may be extensively

ramified. It has no external opening in most instances, so that the eggs only escape from it by the breaking down of the proglottis or by dehiscence. But in some (*e.g.*, *Dibothriocephalus*) it has an independent external opening (Fig. 217, *B*). The female aperture leads into a narrow canal—the vagina—which ends in a receptaculum seminis from which the narrow fertilizing duct conveys the sperms to the oviduct. In a small number of Cestodes the sexes are distinct.

The **development** of some of the Platyhelminthes (Rhabdocœla, monogenetic Trematodes) is direct—*i.e.*, not complicated by the occurrence of a metamorphosis; in the digenetic Trematodes, the Cestodes, and some of the Planarians a metamorphosis occurs.

The eggs of the Polyclads, each of which consists merely of the fertilized

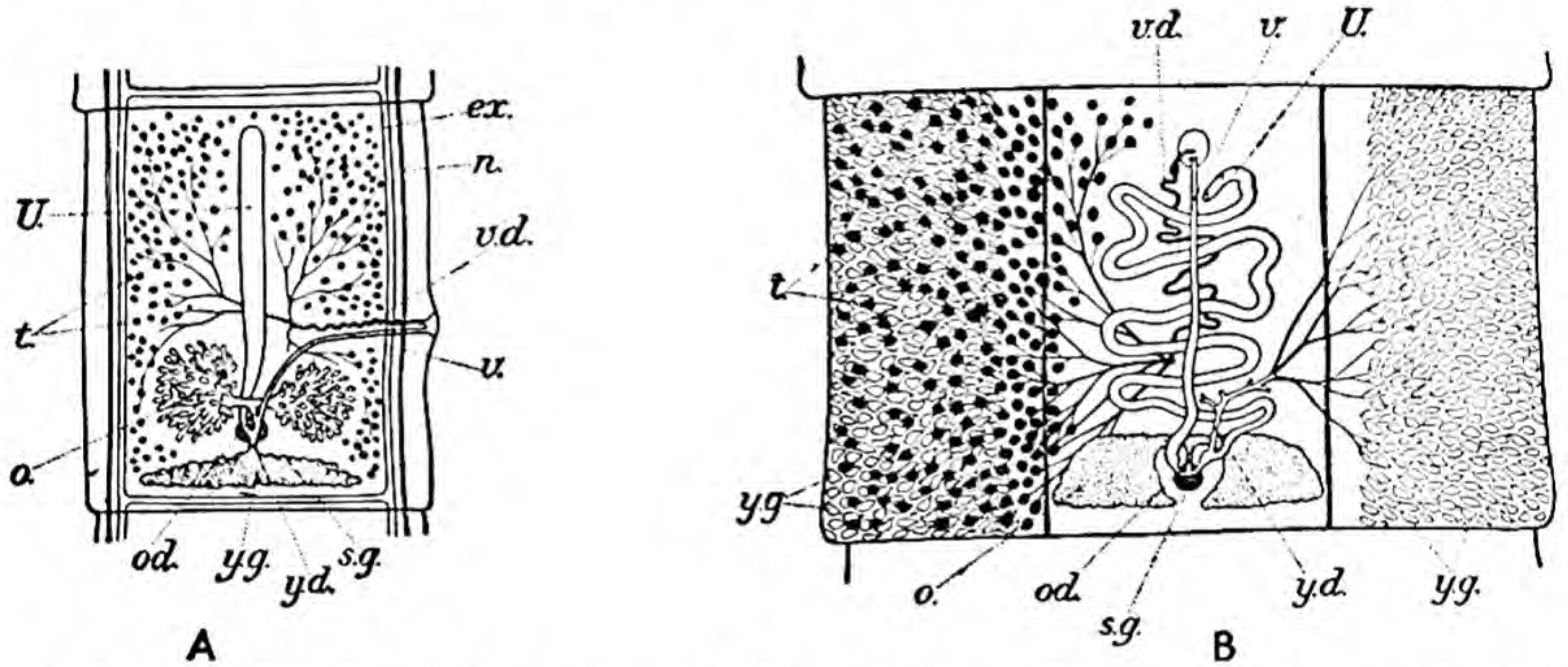


FIG. 217.—Illustrating the arrangement of the genital organs in a sexually mature proglottis of *A*, **Taenia** and *B*, **Dibothriocephalus.** In *B* for the sake of clearness the testes are omitted in the right half of the figure and the yolk-ducts in the left half. *ex.* excretory canal; *n.* nerve-cord; *o.* ovary; *od.* oviduct; *s. g.* shell gland; *t.* testes; *U.* uterus; *v.* vagina; *v. d.* vas deferens; *y. d.* yolk duct; *y. g.* yolk glands. (From Graham Kerr's *Zoology for Medical Students* (Macmillan & Co., Ltd.).)

ovum usually enclosed in an egg-shell, are, in most instances, laid in large numbers embedded in a plate or capsule of slimy secretion. The ovum divides first into two parts, then into four. These are slightly unequal in size, one of them being somewhat larger than the others, and by the position of this and its relations to the other three, the chief axes and planes of the embryo are already determinable at this early stage. In the notation adopted in following out the *cell-lineage* or order of development of cell from cell in the embryo, this largest cell is known as *D*: the other three are *A*, *B*, *C*—the lettering following the direction of movement of the hands of a clock when looked at from above. As shown by subsequent changes, *D* is posterior, *B* anterior, *A* and *C* are lateral. From these four cells, which are called *macromeres*, a succession of four sets of four cells (*quartettes*) is given off at the upper or

animal pole. The cells of the first three quartettes are all smaller than those from which they are derived. They are therefore called *micromeres*. In these divisions the longitudinal axes of the nuclear spindles are not vertical but oblique, with the result that the cells of the newly formed quartettes are situated opposite the furrows which separate the underlying cells of their origin (Fig. 218). From the particular way in which the cells of the quartettes are given off, the type of cleavage here described is known as the *spiral* type. It also prevails in the Annelida and Mollusca.

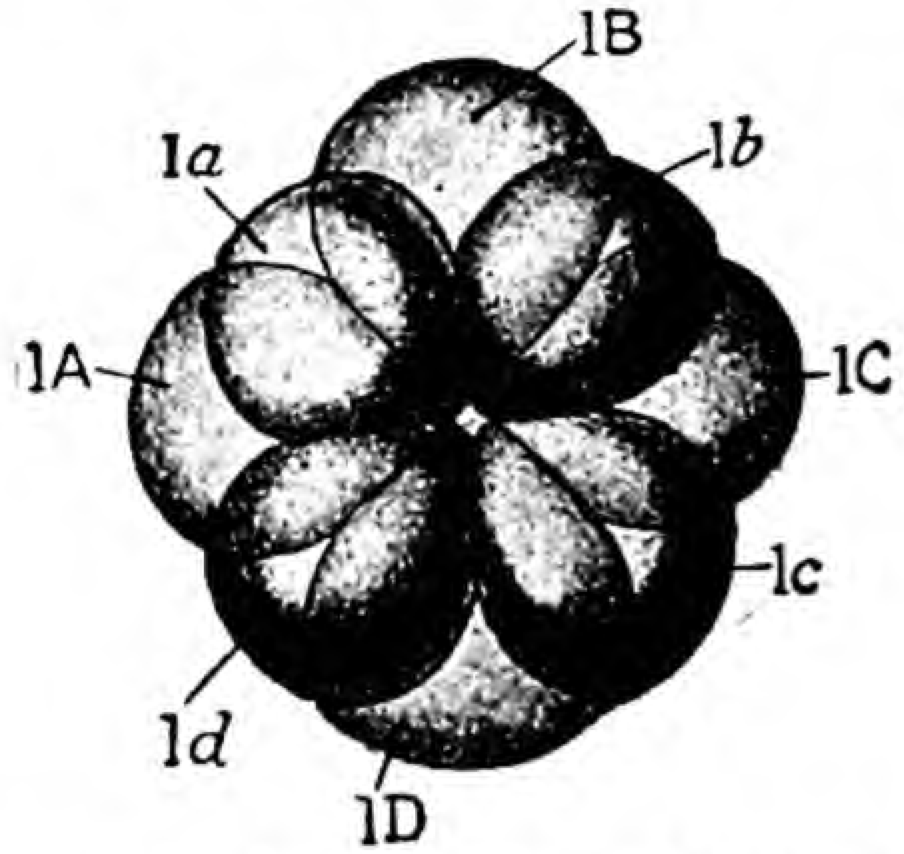


FIG. 218.—Developing egg of **Planocera.** Eight-cell stage viewed from animal pole. (From McBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Surface.)

The members of the first quartette are designated 1*a*, 1*b*, 1*c*, and 1*d*, the small letter of each indicating its derivation from the macromere with the corresponding capital; those of the second quartette are 2*a*, 2*b*, 2*c*, and 2*d*; and so on with the others. The formation of the third quartette results in a stage (Fig. 219) in which the embryo consists of thirty-two cells in all, since the cells of the first and second quartettes divide once again. In later stages the micromeres

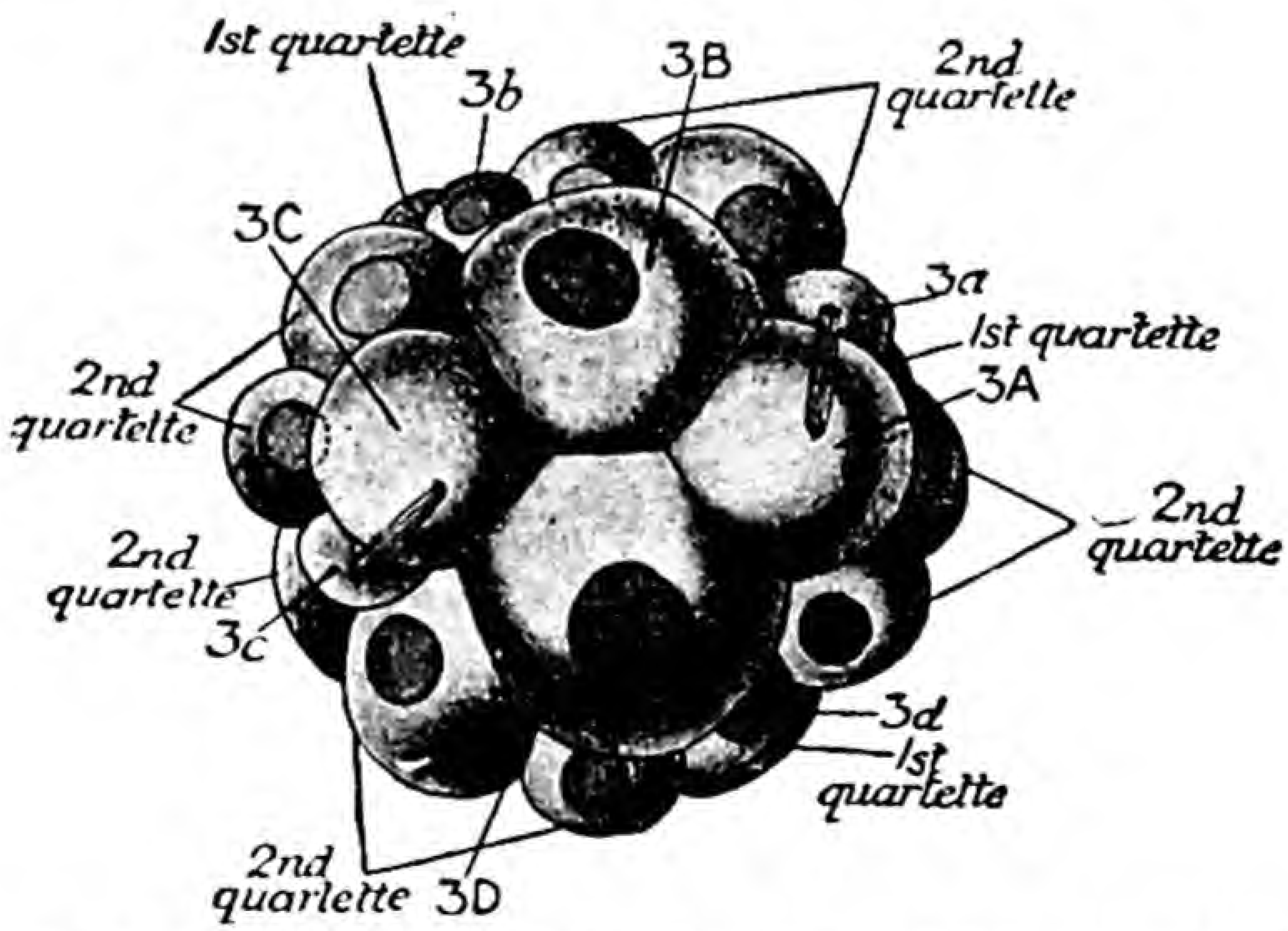


FIG. 219.—Developing egg of **Planocera** : thirty-two cell stage, seen from the lower (vegetative) pole. As the four original megameres, *A*—*D*, have now each given off three cells in succession, their designations are now 3*A*—3*D*. (From MacBride, after Surface.)

increase greatly by further division and extend as a cap, the ectoderm, composed of a single layer of small cells over all the upper part (animal pole) of the embryo; then they spread further as a thin layer over the

entire surface till only a slit-like blastopore is left on the ventral side: finally the blastopore closes and the ectoderm forms a complete investment.

Meanwhile the other embryonic layers have been established. It is one of the cells of the fourth quartette that is alone or mainly responsible for the origin of the endoderm and a great part of the mesoderm. The four original macromeres, *A*, *B*, *C*, and *D*, now reduced to quite small cells (Fig. 220, *mac.*), after the separating off of the fourth quartette take no further part in development, and are ultimately absorbed. Of the four cells of the fourth quartette, which are comparatively large, three become broken up into masses of yolk material to be subsequently absorbed as food; but they may (*Discocœlis*) first give off cells which contribute to the formation of the endoderm. The fourth (designated 4*d*) gives rise, in Planocera, to the whole of the endoderm and a considerable part of the mesoderm. 4*d* divides into two cells, an outer ($4d_1$) and an inner ($4d_2$); the former divides to give rise to the greater part of the endoderm (*end.*). The latter, dividing into two cells, each of which contributes a small cell (*end'.*) to the pharyngeal part of the endoderm, gives rise to two strings of cells (*mes.*) extending obliquely forwards and spreading out to form eventually a continuous layer constituting the greater part of the mesoderm. The mesoderm in the neighbourhood of the stomodæum is independently developed from descendants of the second quartette (*mes. ect.*).

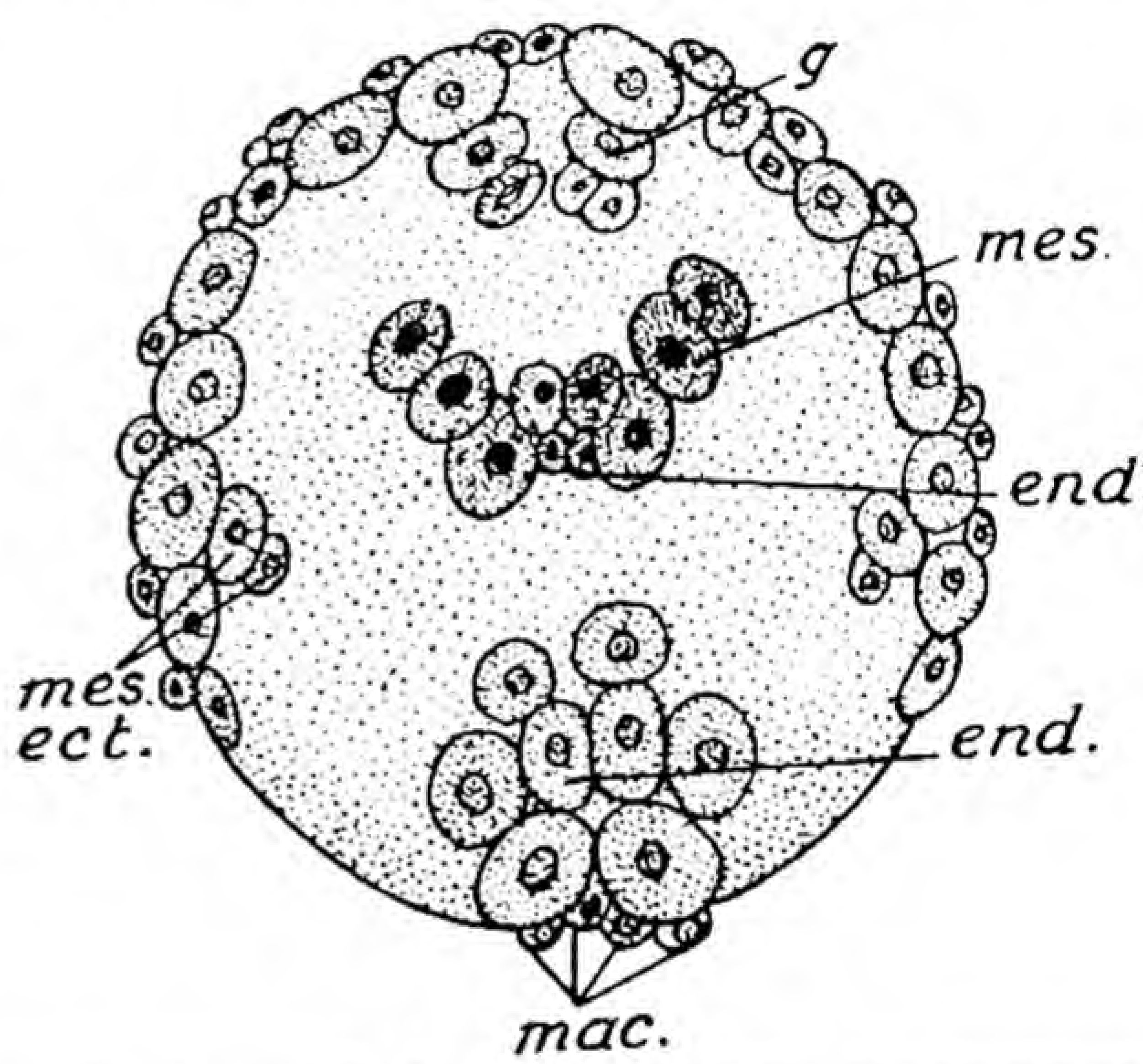


FIG. 220.—Embryo of **Planocera.** Diagrammatic frontal section, passing through animal (upper) and vegetative (lower) poles. *mes.* mesodermal bands (products, with *end'.*, of $4d_2$); *end.* endoderm (products of $4d_1$); *end'.* small endoderm cells formed from mesoderm rudiment; *mac.* vestigial macromeres; *mes. ect.* cells of ectodermal origin derived from the second quartette which migrate inwards to form muscles of the stomodæum; *g.* cells forming rudiment of brain. (From MacBride, after Surface.)

The process by which the germinal layers have become formed is, as in the Ctenophora (p. 205), a process of *epibolic gastrulation*. The brain is developed from a pair of thickenings of the ectoderm (Fig. 220, *g.*): these unite into a common mass from which the longitudinal nerves are formed as backward outgrowths. The mouth is developed as an ingrowth from the ectoderm in the position of the former blastopore, and, as the embıyo becomes flattened, passes from the posterior end to what is destined to be the ventral surface of the worm, while the muscular tissues of the wall of the pharynx are formed

from surrounding mesodermal elements (*mes. ect.*). The intestine is at first simple in form; the cæca are developed as a result of the formation of vertical mesodermal septa which, growing inwards, constrict the enteric wall and the enclosed mass of nutrient material. The embryo, which has assumed an ellipsoidal shape, becomes flattened in the dorso-ventral direction, and, having absorbed the greater part of the nutrient matter, escapes by rupture of the egg-shell (Fig. 221).

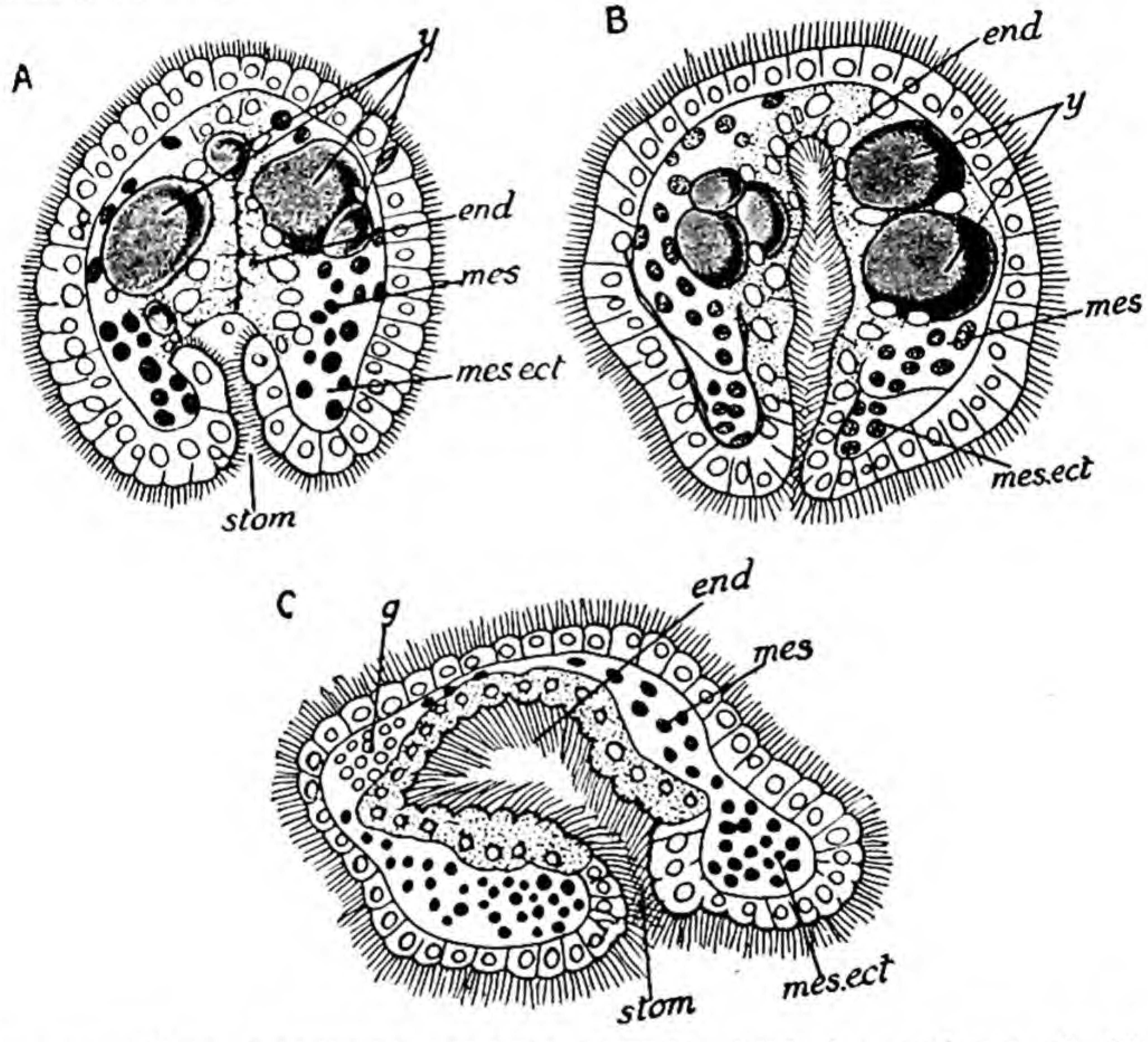


FIG. 221.—Three longitudinal sections through developing embryos of **Planocera.** Letters as in Fig. 220. In addition, *stom.* stomodæum; *y.* yolk spheres resulting from the disintegration of the cells, *4a*, *4b*, and *4c*; *A*, the endoderm forms a solid mass of cells in which the gut-cavity is just beginning to appear; *B*, later stage, the gut-cavity has appeared; *C*, longitudinal section of Müller's larva just after its escape from the egg capsule. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Surface.)

In many cases the embryo develops into a characteristic larval form, such as that known as *Müller's larva* (Fig. 222). It assumes an oval shape, with a series of eight elongated processes, fringed with long cilia connected together into a continuous ciliated band. There are eye-spots at the anterior end and a mouth in the middle of the ventral surface. The form of the body alters after a time, becoming gradually longer and flatter, and the arms are gradually reduced in length, till, eventually, they become completely absorbed.

The development of the Triclads is very different from that of the Polyclads. Each egg-capsule or cocoon encloses a number of fertilized eggs and a quantity of yolk-cells. After cleavage a blastoderm is formed composed of a rounded mass of cells surrounded by the yolk-material, the cells of which become more or less fused. Around the periphery of the blastoderm a layer of cells forms a thin membrane—the provisional ectoderm. About the middle appears a rounded group of cells which passes to the periphery and becomes connected with the ectoderm; a cavity is formed in its interior and it becomes converted into the embryonal pharynx. Meanwhile a group of four cells enclosing a cavity is modified to form the foundation of the endoderm, and increasing in number gives rise to the embryonal intestine, into which the embryonal pharynx soon opens, the latter opening on the exterior by a mouth aperture.

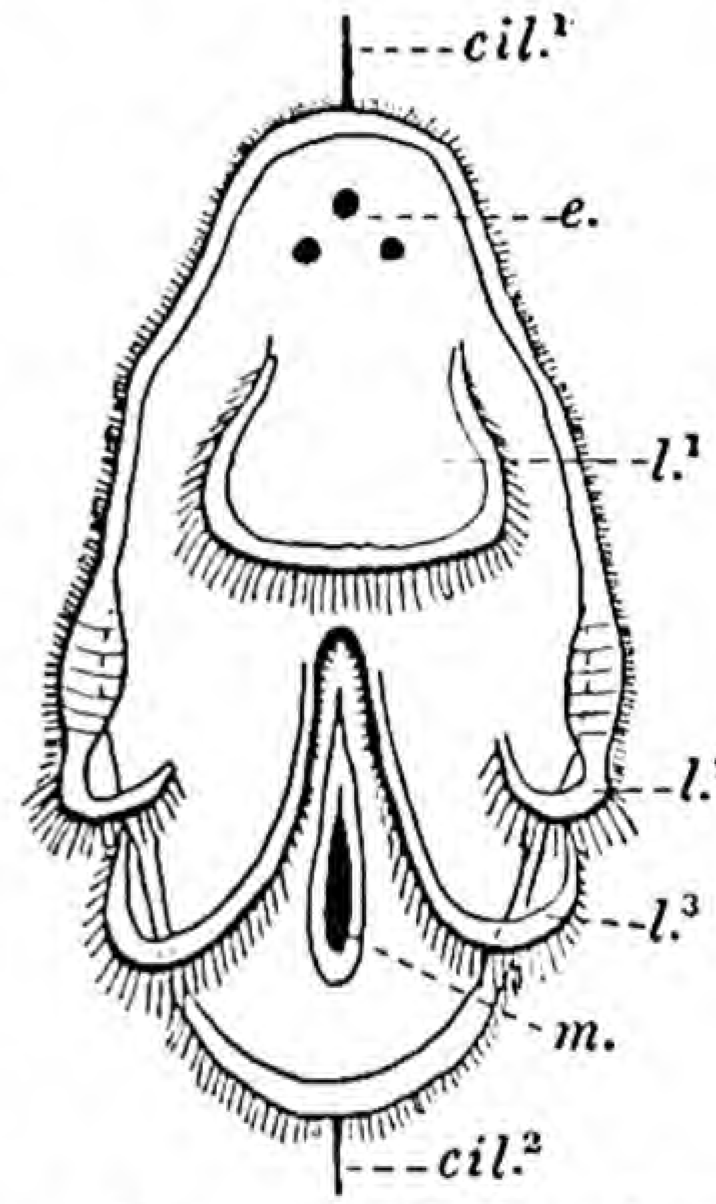


FIG. 222.—Müller's larva of a Polyclad, **Cycloporus papillosus** Lang. Ventral view. *cil.*[1] large cilium at anterior end; *e.* eyes; *l.*[1], *l.*[2], *l.*[3], projecting lobes, the edges of which have cilia longer than those on the general body surface (there are eight of these lobes, there being one similar to *l.*[1] and another pair similar to *l.*[3] on the dorsal surface); *m.* mouth; *cil.*[2] large cilium at posterior end. (From Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge).)

The embryonal pharynx has the function of swallowing the yolk-matter with which the embryonal intestine becomes greatly distended. At a subsequent stage the embryonal pharynx and intestine are aborted, and the former comes to be represented merely by a mass of cells. In this a cavity arises—the cavity of the permanent pharynx. The permanent intestine becomes formed and the cavity of the pharynx opens into its lumen. Subsequently the permanent mouth makes its appearance.

An account has already been given (p. 227, Fig. 192) of the development and metamorphosis of the Liver-Fluke (*Fasciola hepatica*) which may be looked upon as typical of the digenetic Trematodes in general. There is thus to be recognized in the digenetic Trematodes an *alternation of generations* comparable to that which has been described as so general in the Cœlenterata. In the Trematoda, however, it is to be observed, it is an alternation of a sexual, not with an asexual, but with a parthenogenetic generation (the sporocyst), the ova of which develop into a second parthenogenetic generation (the rediæ); and these finally produce larvæ (the cercariæ) capable of developing into the sexually mature form. The term *heterogamy* is applied to a life-history of this kind, in which several distinct generations succeed one another in a regular series.

In some of the Fasciolinæ the eggs, instead of becoming free as in the case of the Liver-Fluke, are taken directly into the digestive canal of the

intermediate host, and there hatched out. The sporocyst stage may take the form of a branching tube in the interior of which cercariæ are developed—the redia stage being omitted. Sometimes the sporocyst becomes directly developed into a redia instead of giving rise to a generation of the latter by such a process of internal development as that described in the case of the Liver-Fluke. The cercariæ in most digenetic Trematodes only develop further if they succeed in establishing themselves in a second intermediate host instead of merely becoming encysted on the surface of herbage, as in the case of the Liver-Fluke. The cercariæ of different Trematodes differ greatly, particularly with regard to the nature of the tail. In some forms the cercaria is tailless: such cercariæ do not become free, but are taken directly—with the intermediate host in which they have been developed—into the digestive canal of the final host.

Among the Monogena, *Gyrodactylus* (Fig. 203, *A*) is viviparous, and the remarkable phenomenon is observed that the embryo (h_1), while still within the body of the parent worm, develops another embryo (h_2) in its interior, and this again develops a third. The rest of the Monogena deposit eggs each of which, within a chitinous shell, contains a fertilized ovum and a number of yolk-cells. Usually there is a stalk, and often an operculum. In general the development appears to be direct; but *Polystomum* passes through a larval stage with five rows of cilia, and in *Diplozoon paradoxum*, a parasite on the gills of certain fresh-water Fishes, in which there is also a ciliated larval stage, the young animals do not become sexually mature until two of them have permanently united with one another.

The egg of a Cestode is similar in essential respects to that of a Trematode: there is a tough, chitinoid membrane or egg-shell, which encloses not only the ovum but a number of yolk-cells. The result of cleavage is the formation of a superficial layer of cells (ectoderm) and a central mass, all enclosed in a membrane composed of a single layer of cells thrown off when the embryo escapes from the egg. The ectodermal cells become ciliated in *Dibothriocephalus*; in others they are thrown off or ultimately absorbed without developing cilia. The central mass of cells alone forms the embryo. The embryo, while still consisting of a small number of cells, develops a series of six chitinous hooks. These early changes all take place in the majority of Cestodes while the egg is still in the uterus of one of the most posterior of the proglottides of the parent worm. When the proglottis in question becomes separated off, and has passed out from the body of the *final host*, the eggs are discharged.

In order that development may proceed further, the embryo must in most cases reach the interior of a second or *intermediate host*. This is a passive migration, since the embryo of the Cestode is still confined within the egg-shell, and the transference has to take place in the water or food. The diges-

tive fluids of this intermediate host dissolve the egg-shell and set free the contained *six-hooked embryo* or *onchosphære*, which bores its way by means of its hooks to some part of the body in which it is destined to pass through the next phase in its life-history, and there becomes encysted.

The phase which follows presents two main varieties. In cases in which the intermediate host is an invertebrate animal, the hooked embryo develops into a form to which the name of *cysticercoid* is given; when, on the other hand, the intermediate host is a Vertebrate, the form assumed is nearly always that termed *cysticercus*, or bladder-worm. The cysticercoid form (Figs. 223

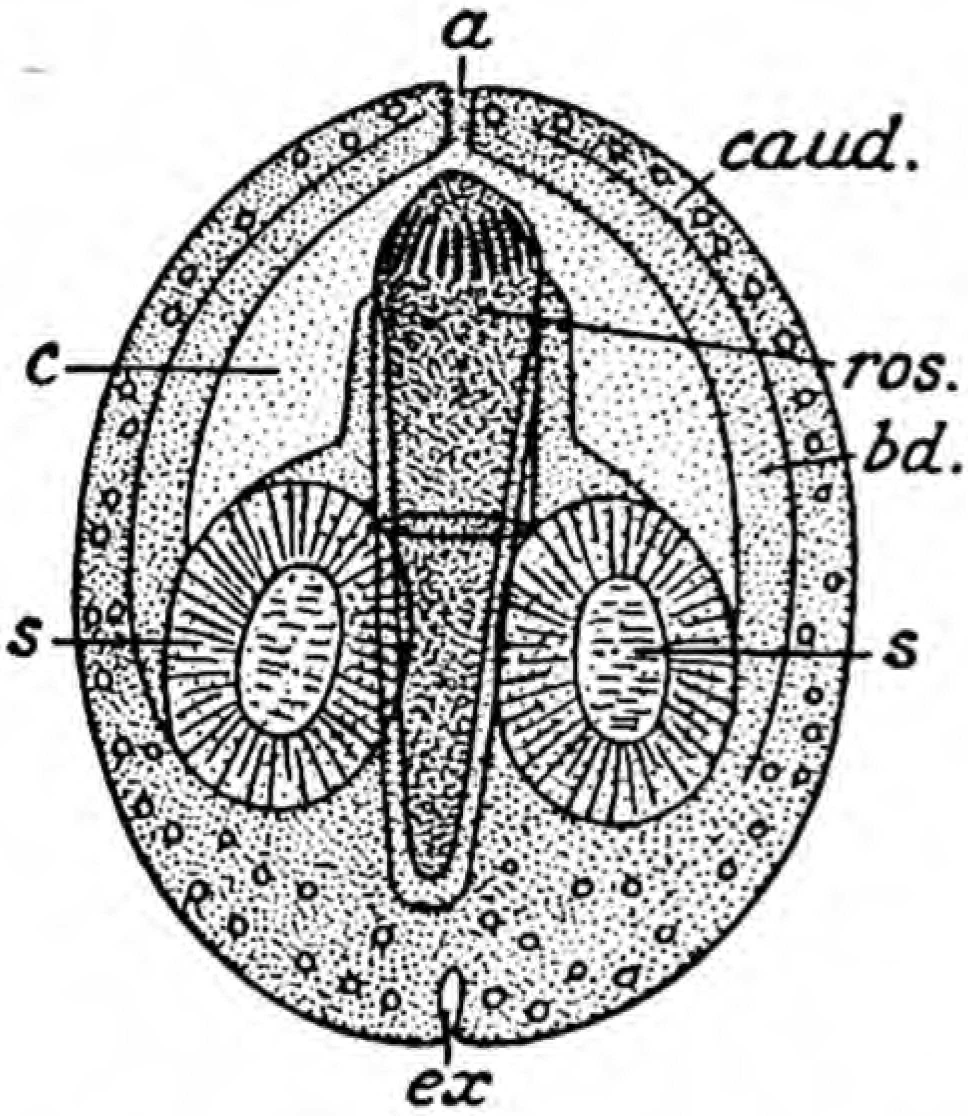


FIG. 223.—A **Cysticercoid** (*Polycercus*) with the head and rostellum enclosed by the caudal vesicle. *a.* aperture through which evagination takes place; *bd.* body; *c.* cavity of cyst; *caud.* caudal vesicle; *ex.* aperture of excretory system; *ros.* rostellum; *s.* sucker. (After Haswell and Hill.)

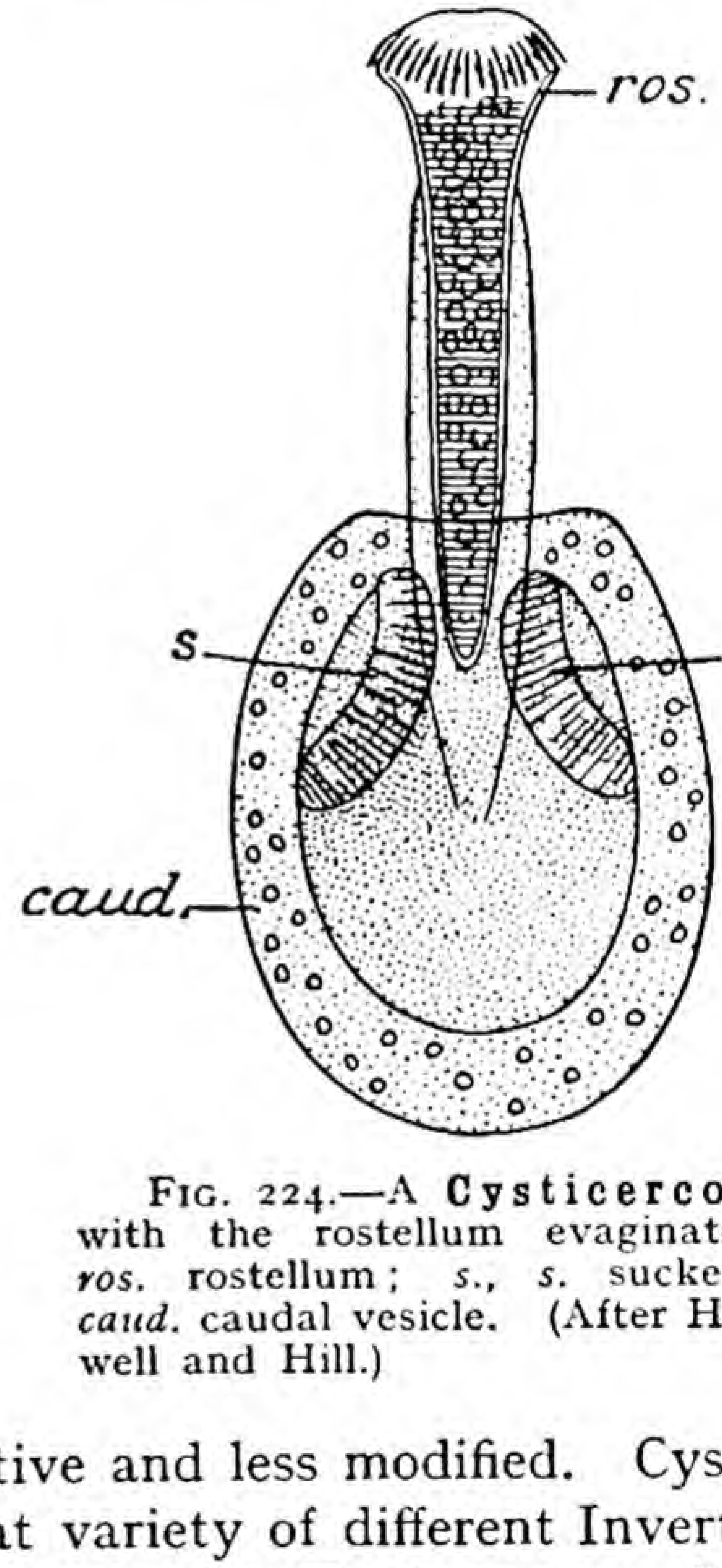


FIG. 224.—A **Cysticercoid** with the rostellum evaginated. *ros.* rostellum; *s., s.* suckers; *caud.* caudal vesicle. (After Haswell and Hill.)

and 224) is to be regarded as the more primitive and less modified. Cysticercoids of various tape-worms occur in a great variety of different Invertebrates—*e.g.*, Insects of all kinds, Water-fleas, Centipedes, Earthworms. The hooked embryo loses its hooks and develops into the cysticercoid in some part of the invertebrate intermediate host. The cysticercoid consists of three parts—a tape-worm *head* or *scolex* with the hooks and suckers of the mature worm, a so-called *body*, and a *caudal vesicle*. Sometimes there is a tail recalling to some extent the tail of a cercaria. Sometimes the caudal vesicle is absent: when present, either from the first, or as a result of later changes, it encloses the head as well as the body after the manner of a cyst. While undergoing these changes the cysticercoid is usually enclosed in an adventitious cyst

formed for it by the tissues of its host, but it often lies free in the body-cavity. The transference to the final host is effected by the intermediate host, or the part of it containing the cysticercoid, being taken into the alimentary canal of the final host. Sometimes, if the intermediate host is a relatively small animal, such as a water-flea, this may take place " accidentally " ; in other cases the invertebrate intermediate host actually forms the food of the final host. Thus a cysticercoid having as an intermediate host an Earthworm is taken with the latter into the alimentary canal of a Sea-Gull—its final host. In this way the cysticercoid is set free in the alimentary canal of the final host, the head becomes pushed out from the enclosing caudal vesicle and body (probably owing to the stimulus of the higher temperature), so that the suckers and hooks come into play and attach the young tape-worm to the wall of the alimentary canal.

The *cysticercus* or bladder-worm differs from the cysticercoid mainly in its much greater size and in the development of a relatively large caudal vesicle or caudal bladder. When the hooked embryo has reached that part of the vertebrate host in which it is destined to develop into the cysticercus it undergoes a remarkable change ; it becomes greatly enlarged, and a cavity, filled with fluid or with a very loose form of connective-tissue, appears in its interior, so that it assumes the appearance of a relatively large bladder. On one side of this bladder appears a small invagination with a cavity opening freely on the exterior. On the bottom of this is formed an elevation projecting into its interior ; this is the rudiment of the rostellum on which the hooks are borne ; at its base, on the inner surface of the side walls of the invagination, appear the suckers. When inverted this invagination corresponds closely with the head and body of the cysticercoid ; the bladder corresponds to the caudal vesicle. Thus the chief difference between a cysticercus and a cysticercoid is that in the former the caudal vesicle is relatively very large and that the order of development of the parts is somewhat modified.

A very small number both of cysticercoids and cysticerci multiply by proliferation—by the formation of more than one tape-worm head from one embryo. In the few instances in which this occurs among the cysticercoids the hooked embryo gives rise, not directly to a cysticercoid, but to a mass of cells from which are given off a number of buds, each developing into a cysticercoid with the three parts already described. One such form occurs in certain Earthworms, another in a Myriapod (*Glomeris limbatus*).

Tænia cœnurus of the Dog has a bladder-worm stage in the Sheep and Rabbit which gives rise to several tape-worm heads, and the same holds good of *Tænia serialis* from the Fox. But the best known instance of multiple production of scolices in a cysticercus is *Tænia echinococcus*—well known as cause of the disease termed *hydatids*, common in Man and in various domestic animals. In this case the hooked embryo develops into a large *mother-cyst*,

from the interior of which *daughter-cysts* are budded off (Fig. 225). Eventually from the walls of these daughter-cysts there are formed numerous tape-worm heads, or *scolices* (Figs. 226 and 227), which, when fully formed, assume the appearance of cysticercoids without the caudal vesicle. These are readily detached, and should the organ in which the cyst has been developed be

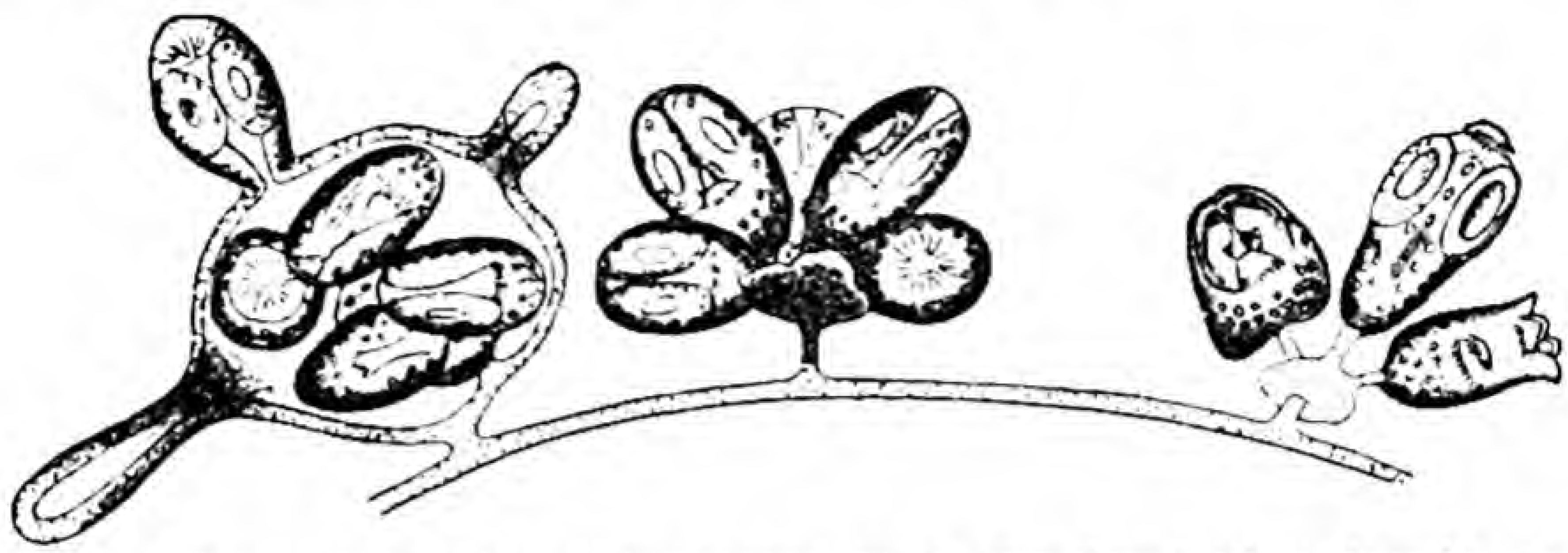


FIG. 225.—Cyst of **Tænia echinococcus** with the developing daughter-cysts and scolices. (After Leuckart.)

devoured by a Dog—which is the final host of the parasite—some of these scolices become attached to the wall of the intestine and develop into the adult *Tænia echinococcus*—which are very small as compared with the size of the cyst and as compared with other tape-worms. The eggs, passing out

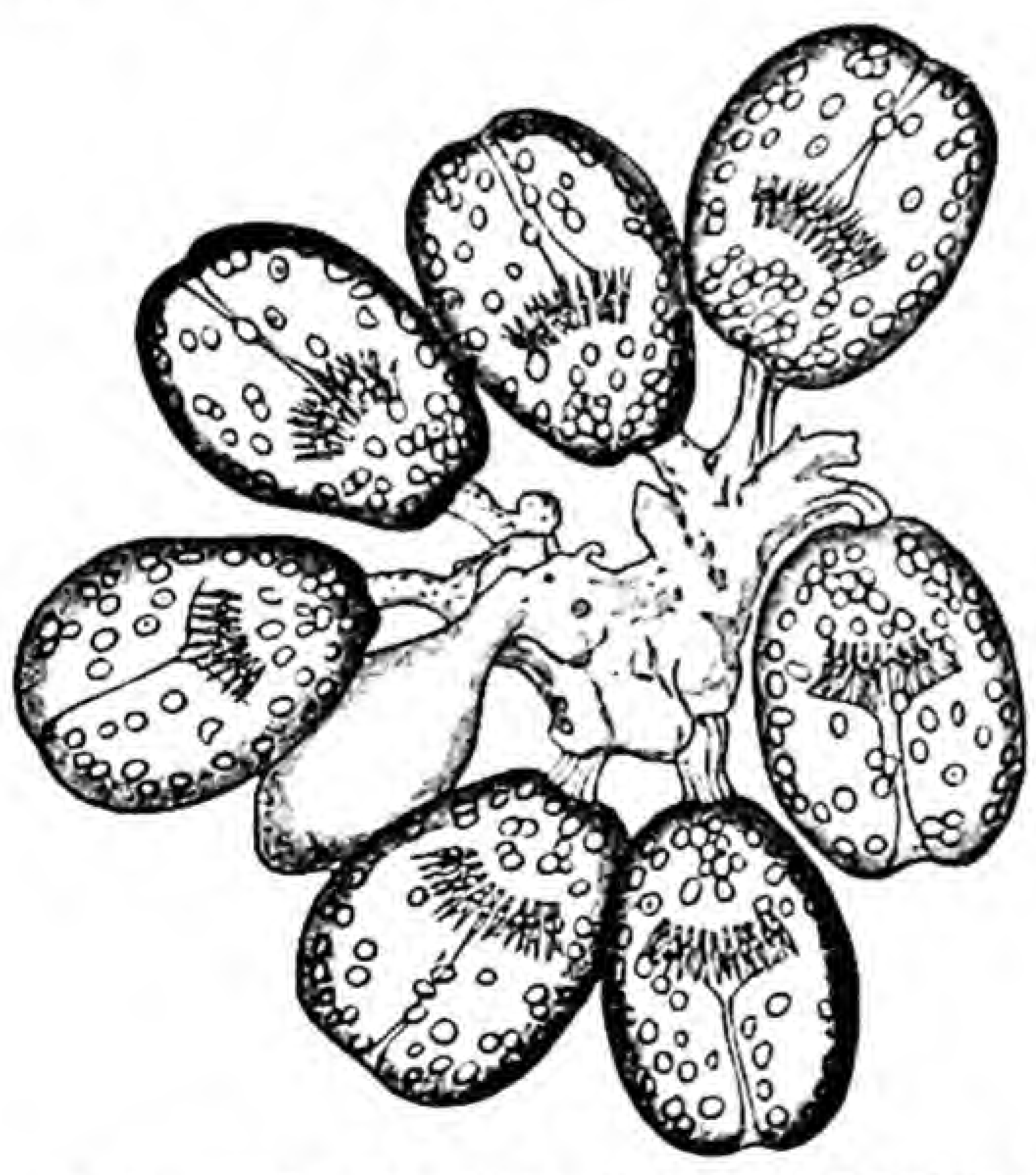


FIG. 226.—Scolices of **T. echinococcus.** (After Cobbold.)

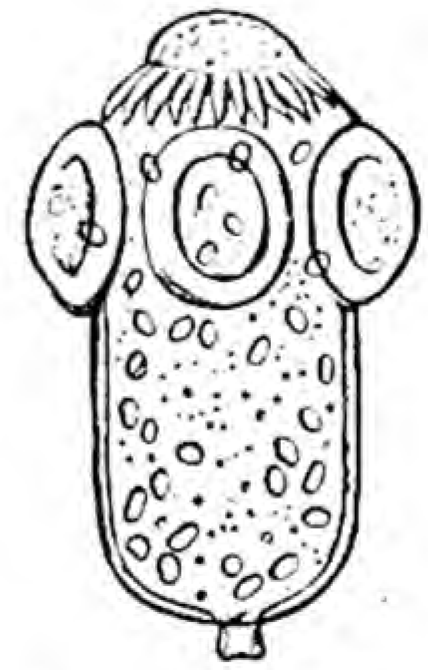


FIG. 227.—Separate scolex of **T. echinococcus.** (After Cobbold.)

with the fæces of the Dog, may be taken into the digestive canal of Man or of one of the domestic animals, and the minute embryos escaping, reach some organ, such as the liver, lung, or brain, in which they are capable of developing into a comparatively enormous cyst.

Asexual reproduction also occurs in some Platyhelminthes. In some

Rhabdocœle Turbellaria (*Microstomum*) a process of budding (Fig. 228) results in the formation of strings of sexual individuals which may eventually separate; the new bud is always formed from the posterior end of the last individual of the string.

The sporocyst stage in the Trematodes may, as already mentioned, multiply by budding or fission. The formation of new proglottides in the Tape-worm may be looked upon either simply as growth accompanied by segmentation, or as asexual multiplication, according as we regard the proglottides as *segments* of a simple animal or as *zooids* of a colony. There is this essential difference between the formation of proglottides and the asexual multiplication by budding in Microstomum, that in the former case the proglottides, when they have been formed by segmentation of the undivided part behind the head, do not in turn give rise by budding to new proglottides. Spontaneous transverse fission has been observed in certain Tricladida, and is often followed by the regeneration of the lost portion.

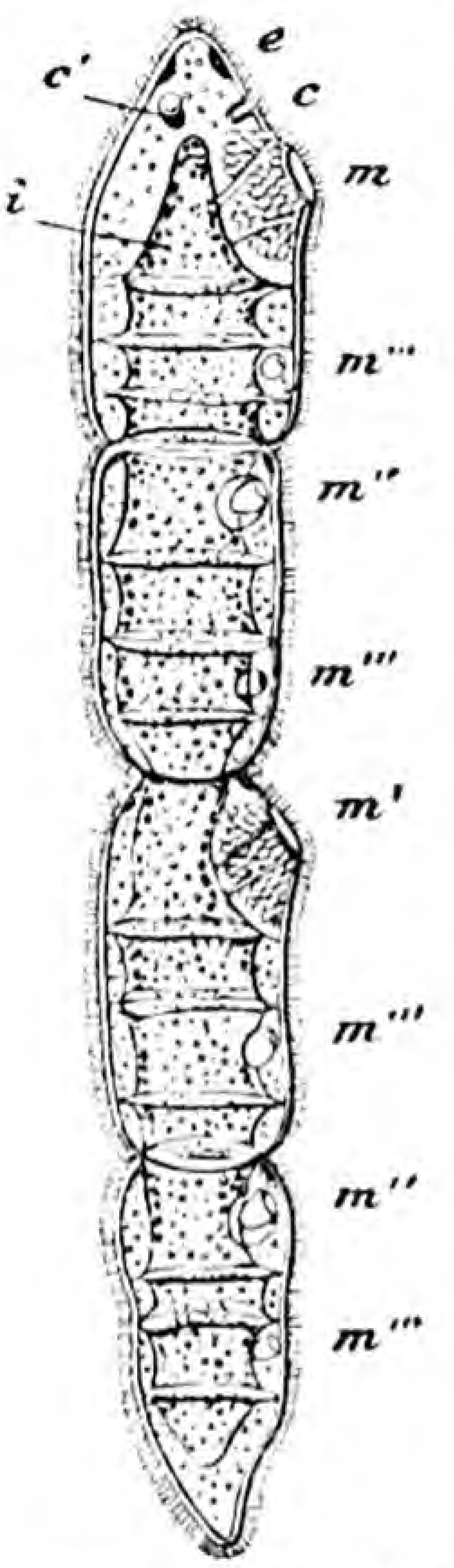


FIG. 228.—Process of budding in **Microstomum.** *c.*, *c'.* ciliated groove; *e.* eye-spot; *i.* intestine; *m.*, *m'.*, *m''.*, *m'''.* mouth. (After Von Graff.)

6. Distribution, Mode of Occurrence, and Mutual Relationships.

Of all the great groups of the animal kingdom above the Protozoa the Platyhelminthes are the widest in their *distribution*. Members of the phylum occur on land, in fresh water down to the bottom of some of the deepest lakes, on the sea-shore, in the deep sea, and on the surface of the ocean; and parasitic Flat-Worms live, in one phase or another, in animals of nearly every class of the Metazoa.

As regards their *mode of life*, they present almost every possible gradation between free-living forms which procure their food—consisting of minute animals and plants—by their own exertions, and forms that are only capable of living in a special part of the interior of a certain other animal, and are quite incapable of procuring food for themselves, living by the passive absorption of the juices of their host or of its digested food. The Turbellaria are for the most part free-living, and their food consists of small Crustacea or the larvæ of larger forms, Insect larvæ, Water-mites, Rotifers, small Worms, and the like; or sometimes of Diatoms and minute Algæ of various kinds. Some, however, live a life of true parasitism. Such are certain Rhabdocœles which are parasitic in the alimentary canal of various Sipunculids and Holothurians, and in the liver of Gastropods. In these there is correlated with the inactive

mode of life a tendency to degradation of structure, a degradation which is characteristic of parasites in general: the pharynx is reduced in size as compared with that of non-parasitic allied forms, not being required for the capture and swallowing of living prey; and the eyes, useless to an animal living in complete darkness, are absent. Some of the Turbellaria, though not parasitic in the strict sense, live in a state of *commensalism* with another, larger animal: that is to say, are more or less constantly associated with it, living on its surface or in one of its cavities that open freely on the exterior, and often sharing its food. An example of this mode of life is the Triclad *Bdelloura*, which lives on the surface of the King-Crab (*Limulus*). The *Temnocephalidæ* living on the suface of the "host" animal, deposit their eggs there, and being carried about by it, subsist on minute living animals captured in the water.

While a free existence is the rule in the Turbellaria, true parasitism is universal in the Trematodes and in the Cestodes. The majority of the monogenetic Trematodes are external parasites, living on a part of the outer surface of a larger animal, and feeding on mucus and other secretions of the integument. Many are parasites on the gills of Fishes. A few, however, inhabit the interior of various organs, and are true internal parasites: one, for example (*Polystomum*), lives in the urinary bladder of the Frog; another (*Aspidogaster*) lives in the pericardial cavity of a Fresh-water Mussel.

The digenetic Trematodes are all internal parasites, and in the adult condition inhabit, in nearly all cases, the alimentary canal, liver, or lungs of some vertebrate animal, swallowing the digested food or various secretions of their host. But, as mentioned before in the account given of their development, they are internal parasites, not only in the adult condition, but throughout the greater part of their life. After a short period of freedom as ciliated larvæ, they again enter into a state of parasitism as sporocysts or rediæ in a second host; and, after a second free interval as cercariæ, may enter the body of a third host to become encysted. The second host is, very generally, a Mollusc, and the cercaria may become encysted in the same animal.

The Cestodes are, of all the Platyhelminthes, those that are most modified in accordance with the condition of internal parasitism in which they remain throughout life. The adult Cestode is almost always an inhabitant of the alimentary canal of a Vertebrate. The intermediate host is frequently also a Vertebrate—commonly of a kind which is liable to become the prey of the final host. In the case of *Tænia crassicollis* of the intestine of the domestic Cat, for example, the cysticercus stage occurs in the livers of Rats and Mice; the cysticercus of *Tænia serrata* of the Dog is found in Hares and Rabbits. But in many cases the intermediate host is an Invertebrate. In either case the passage from one host to another is a passive *translation*, not an active *migration* as in the Trematodes.

A few human parasites belong to the Trematoda, but none that are of very common occurrence among Europeans. *Fasciola hepatica* has occasionally been found in the human liver; *Distomum rathousii* is a common intestinal parasite in China; *Opisthorchis sinensis* occurs in the liver of Man in China and Japan; *Dicrocœlium lanceatum* and various species of the genus occasionally occur in the human subject. *Schistosomum hæmatobium* (Fig. 229) and *S. japonicum*, otherwise known as *Bilharzia hæmatobia*, and *B. japonica*, which differ from most other Trematodes in being unisexual, are found in pairs in the sub-mucous tissue of the human urinary bladder or rectum in various parts of Africa and South America, in Arabia, the Philippines, and Japan. Eggs with contained larvæ are voided with the urine, and if they reach water, the ciliated larvæ or miracidia penetrate into the interior of a fresh-water snail and give rise to sporocysts from which cercariæ are developed. The latter become free, and, if the opportunity presents itself, may enter the human body through the skin or the mucous membrane of the mouth, and, entering the venous system, find their way usually to the veins of the bladder or the large intestine and thence to the sub-mucous tissue, where they become sexually mature.

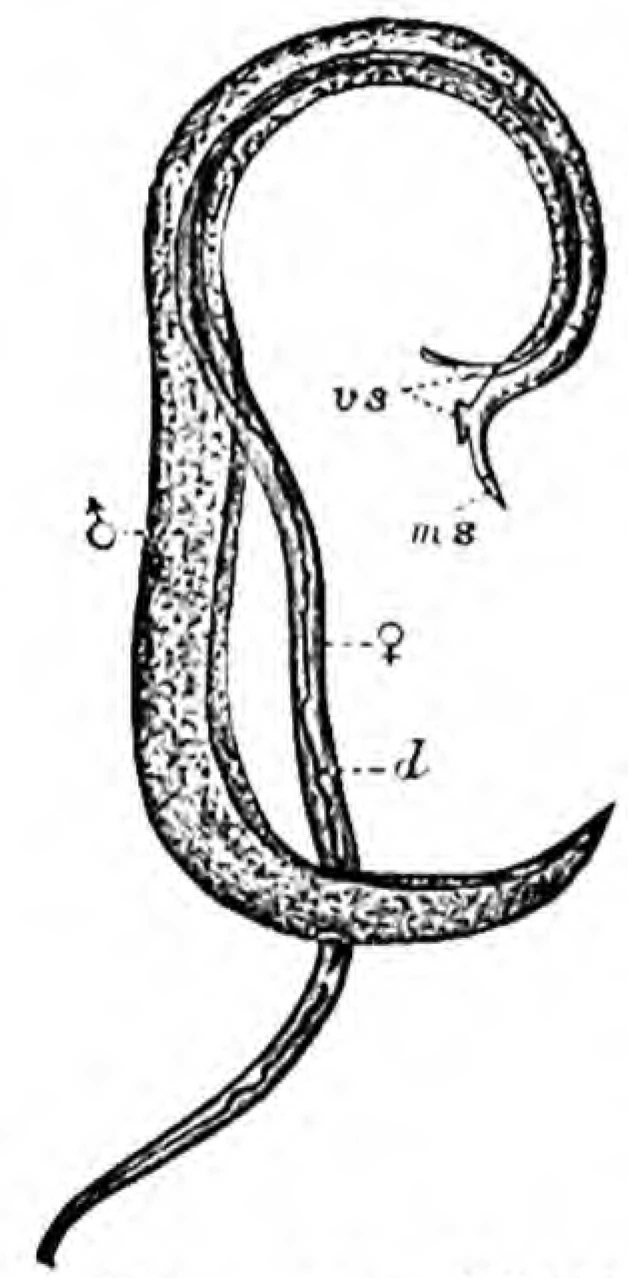


FIG. 229.—**Schistosomum hæmatobium.** The female (♀) lying in a ventral groove of the male (♂). *d.* alimentary canal; *ms.* oral sucker of male; *v. s.* ventral suckers. (After Leuckart.)

The commonest human Cestode parasites among Europeans are *Tænia solium* and *T. saginata*. The cysticercus stage of *T. solium* (*Cysticercus cellulosæ*) occurs, as already stated, chiefly in the muscles of the Pig, that of *T. saginata* in the muscles of the Ox; and the relative prevalence in different countries of these two Tape-Worms varies with the habits of the people with regard to flesh-eating: where more swine's flesh is eaten in an imperfectly cooked state *Tænia solium* is the more prevalent; where more beef, *T. saginata*. *Dibothriocephalus latus*, a very large Tape-Worm without hooks, and with a pair of longitudinal sucking-grooves on the head instead of ordinary suckers, is a common human parasite in Eastern countries. Its cysticercus, which is elongated and solid, occurs in the Pike and certain other fresh-water Fishes.

Of all the Cestode parasites of man, however, the most formidable is one which occurs in the human body, not in the sexually mature or strobila condition, but in that of the cysticercus. This is *Tænia echinococcus*, the presence of which produces what is termed hydatid disease (p. 260). The adult *Tænia echinococcus* is a very small tape-worm with only three or four proglottides, occurring in the intestine of the domestic Dog. The eggs passing out with a

liberated proglottis in the fæces may reach the alimentary canal of Man uninjured in drinking water, on the surface of salad vegetables, and the like; and, the egg-shells becoming dissolved, the contained hooked embryos bore their way to the liver or the lungs or the brain. Arrived at its final destination, the embryo develops into a cyst, which may become of enormous size. In the interior of the *primary* or *mother-cyst* are developed a number of *secondary* or *daughter-cysts*, and from the walls of these, both internally and externally, are formed very numerous scolices in the way already described. Hydatid cysts are very common in some domestic animals (Oxen, Sheep), as well as in Man. Various other Cestodes occur in the bladder-worm stage occasionally in Man—*e.g.*, the *Cysticercus cellulosæ* of *Tænia solium*.

The most primitive of the Platyhelminthes are, without doubt, some of the simplest Turbellaria, and it is among these that we must look for the nearest existing relatives to the Cœlenterata. In none, however, is the relationship very close. *Cœloplana* and *Ctenoplana* are probably rather to be looked upon as Ctenophores specially modified in accordance with a creeping mode of progression than as intermediate forms between Ctenophores and Turbellaria. The relationship with the Cœlenterata is shown, perhaps, most strikingly when we take into account the development of the Turbellaria, in the earlier stages of which there is to be recognized a marked tendency towards a radial symmetry. In their development the Turbellaria, that is to say the Polyclads, show some special points of resemblance to the Ctenophora; the ectoderm cells are formed and spread over the rest in a similar way, and the bands of cilia have a disposition and mode of movement that strongly bring to mind the ciliary swimming plates of the Ctenophora. But though there is much to be said in favour of the view that the Turbellaria and the Ctenophora were derived from a common, not very distant, stock, the latter are too specially modified to be looked upon as the direct ancestors of the former.

The connection between the Turbellaria and the monogenetic Trematodes is very close—so much so that it is difficult to give any characters of universal occurrence distinguishing all the members of the two classes. Thus the Temnocephalidæ which have been included amongst the Turbellaria were formerly regarded to be Trematodes. The Trematodes are, in fact, to be looked upon as Turbellaria some of whose external characteristics—and, in the case of the Digena, whose life-history—have been specially modified in accordance with a parasitic mode of life. It is not unlikely that the Trematodes may be a *polyphyletic* group—*i.e.*, that different families may have become developed from different families of Turbellaria altogether independently, some of them appearing to be nearer the Rhabdocœles, others nearer the Polyclads, and others, again, nearer the Triclads, in the majority of their characters.

The remarkable life-history of the digenetic Trematodes may, as already

pointed out, be looked upon as a special form of alternation of generations—the alternation of a *sexual* with a *pædogenetic* and *parthenogenetic* generation (heterogamy). The sporocyst and redia are to be regarded as intercalated stages—as cercariæ which exhibit pædogenesis. The cercaria is the characteristic larval stage of the Trematodes, and corresponds to the cysticercus or cysticercoid of the Cestode. The most important difference between these is the presence in the former of an enteric cavity, and its absence in the latter. There seems to be something to be said in favour of the view that the enteric cavity of the cercaria is represented by the frontal sucker of some scolices, and by the rostellum of the majority.

Between the adult Cestodes and the Trematodes an intimate relationship is traceable. *Gyrocotyle* (Fig. 212) and *Amphilina* are Cestodes which, but for the absence of an enteric cavity and the want of organs of adhesion at the posterior end, are not far distant from the Trematodes. The most important difference between a Cestode and a Trematode, in addition to the absence of an enteric cavity in the former and its presence in the latter, is the occurrence in the Cestodes of strobilation. *Ligula* in a certain sense forms a connecting link in this respect between the Trematode and the ordinary Cestode, the body being elongated and the reproductive organs repeated as in the normal Tape-Worm, but there being no corresponding division of the body into a string of definitely separated proglottides.

APPENDIX TO THE PLATYHELMINTHES.

THE NEMERTINI.

General Features.—The Nemertines are non-parasitic, unsegmented worms, most of which are marine, only a few forms living on land or in fresh water. They are commonly looked upon as nearly related to the Turbellaria and were formerly included in that class; but in some respects they are higher in organization than the Turbellaria, and they exhibit certain special features distinguishing them from the rest of the lower Worms.

The body (Fig. 230) is nearly always narrow and elongated, cylindrical or depressed, unsegmented and devoid of appendages. In length it varies from a few millimetres to as much as twenty-seven metres. In some cases there is a short narrower posterior region or " tail "; a head is rarely marked off from the body proper. The entire surface is covered with vibratile cilia, and frequently the integument is vividly coloured. Gland-cells of the epidermis secrete a mucous matter, which may serve as a sheath or tube for the animal. The *mouth* (*m.*) is at or near the anterior extremity on the ventral aspect. Near

it in front (rarely united with it) there is an opening through which can be protruded a very long muscular organ, the *proboscis* (*pr.*), the possession of which is one of the most characteristic features of this class of Worms. The proboscis is hollow; when extended to its utmost, a part still remains which is not capable of being everted. This hollow tube (Fig. 231) is open in front, where its edges are continuous with the body-wall, and closed behind. Its wall in the eversible part consists of an epithelium (internal when at rest) continuous with the epidermis and similar to the latter, a basement membrane, and either two or three layers of muscle, circular and longitudinal, with an external thin epithelium of flat cells. The circular muscular fibres are not continued back on the non-eversible part, but the longitudinal fibres pass backwards to form the *retractor muscle*, by means of which the proboscis is attached to the sheath in which it is enclosed, and by means of which also it is retracted. The internal epithelium of the proboscis develops variously formed and arranged papillæ, and in most cases its cells form rods of a similar character to that of the rods or rhabdites of Turbellaria. In the part between the eversible and non-eversible regions—a part which may itself become elongated and complicated in structure—is developed in many Nemertines (*Metanemertini*) a median calcareous stylet (Figs. 234, 235) with groups of smaller accessory stylets at the sides. In the everted proboscis these are borne at the free anterior extremity, and are thus capable of being used as weapons. In *Drepanophorus* there are a number of small stylets supported on a narrow curved plate, together with accessory stylets. In the rest of the Nemertines stylets are not developed. It is by contraction of the muscular walls of the sheath, the cavity of which (*rhynchocœle*) contains a corpusculated fluid, that the proboscis becomes everted. The abundant nerve-supply of the proboscis points to its being used partly as a tactile organ.

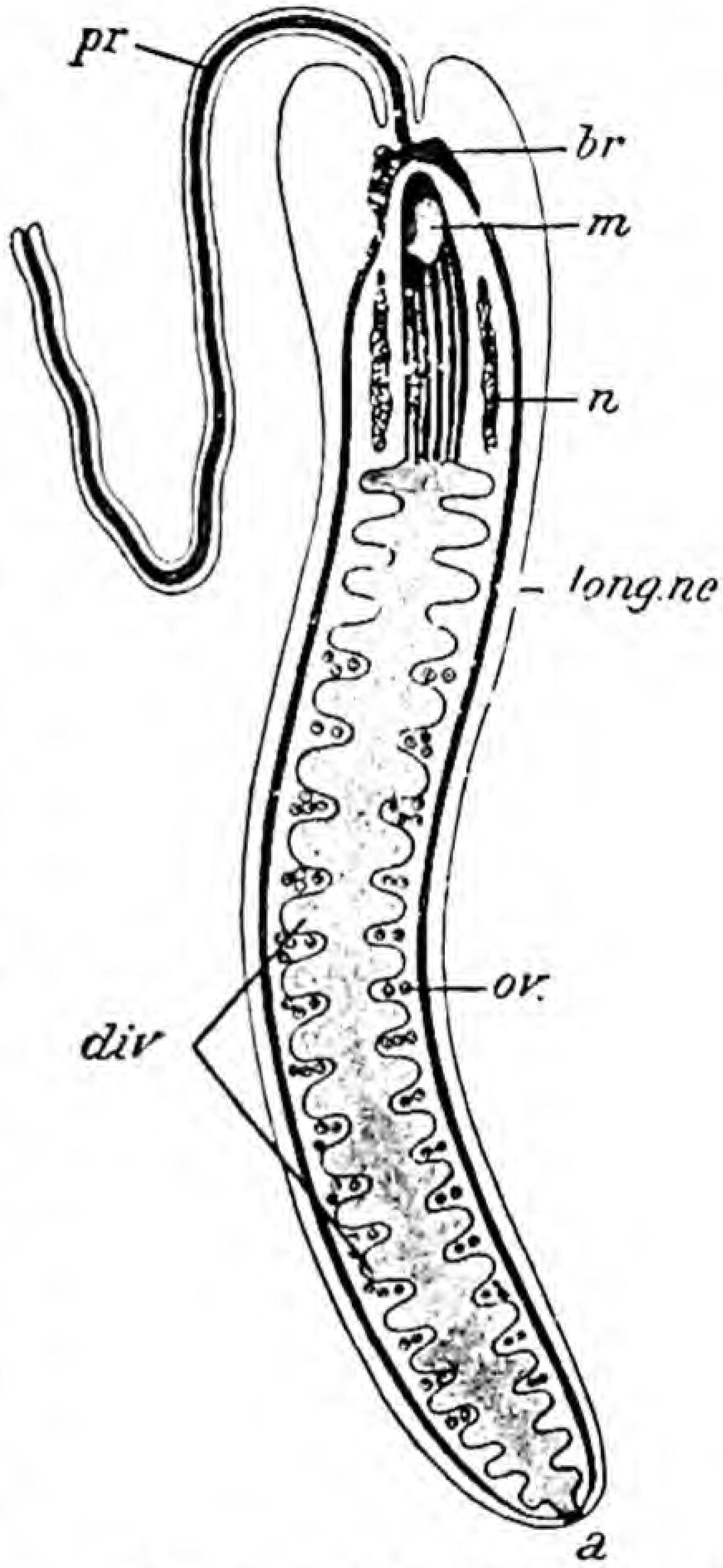


FIG. 230.—Diagram of the organs of a Nemertine, from below. *a.* anus; *br.* brain; *div.* cæca; *long. ne.* longitudinal nerve-cords; *m.* mouth; *n.* excretory organs; *ov.* ovaries; *pr.* proboscis. (After Hubrecht.)

The outermost layer of the **body-wall** is an epidermis of columnar cells, many of which are ciliated, while others are unicellular glands, some of which are arranged in groups; these secrete the mucus with which the surface is usually

covered, and which may form a gelatinous tube. Beneath the epidermis is a basement membrane, very thin in most cases, followed by the muscular layers. In some Nemertines (whence called *Dimyaria*) there are only two layers of muscular fibres, an outer circular and an inner longitudinal; in the rest (*Trimyaria*) a third (longitudinal) layer is superadded. Another circular layer of muscular fibres closely encompasses the digestive canal. The interspace enclosed by the outer muscular layers does not comprise any cavity corresponding to a true cœlome or body-cavity, the interspaces between the organs being filled with parenchyma (Fig. 236).

The **digestive canal** consists of a tube which extends throughout the length of the body from the mouth—situated near the anterior extremity on the

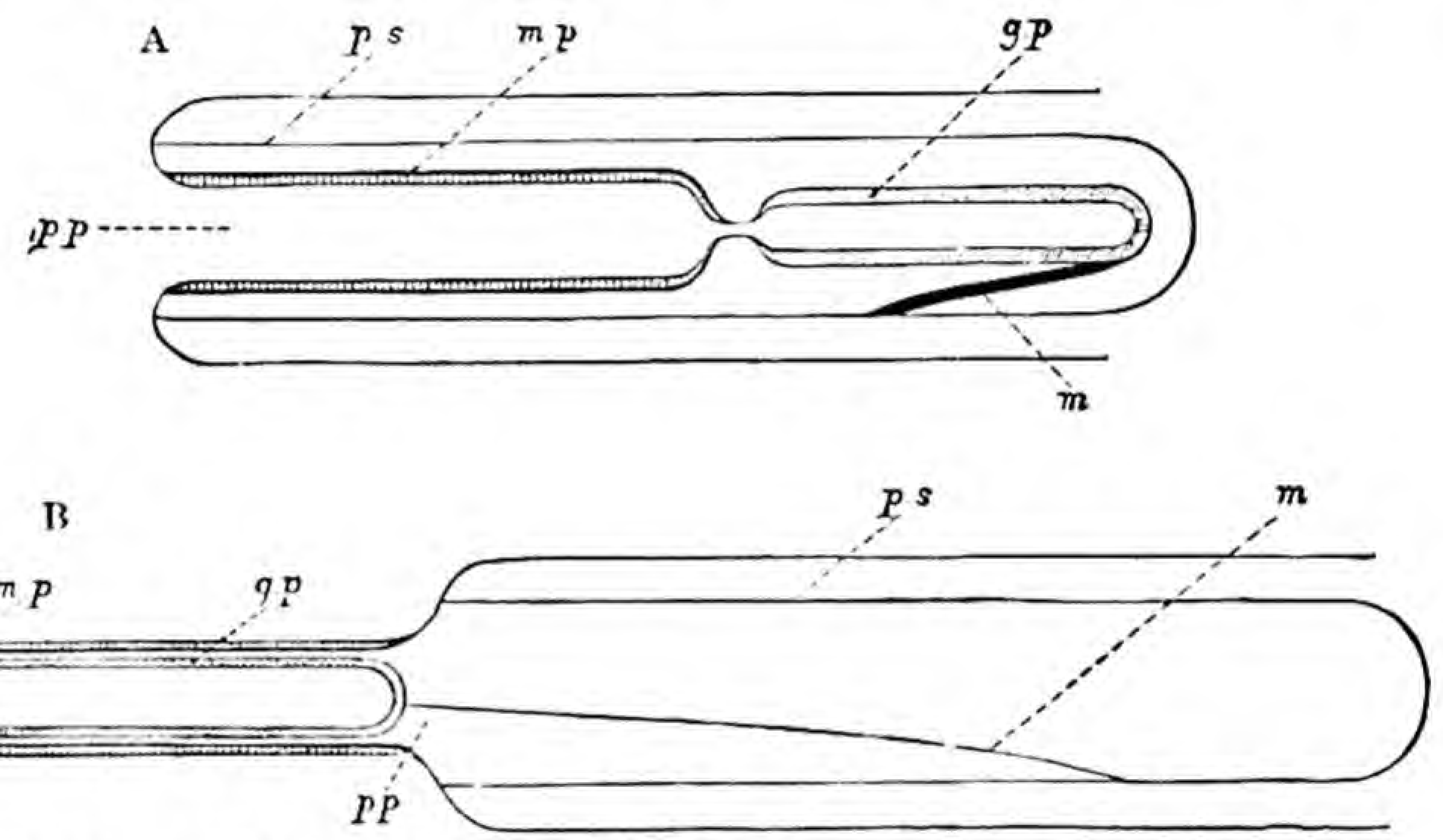


FIG. 231.—Diagrammatic representation of proboscis; (*A*) in the retracted condition, (*B*) in the everted condition. *g. p.* glandular portion of the proboscis; *m.* muscle attaching the proboscis to its sheath; *m. p.* muscular portion of the proboscis; *p. p.* in *A*, proboscis pore; *p. p.* in *B* represents the position of the proboscis pore in the retracted condition of the proboscis; *p. s.* proboscis sheath. (After Sheldon.)

ventral side—to the anus at the posterior extremity.[1] The mouth is usually placed some distance behind the proboscis pore, but may be shifted forwards so as to lie close to the latter, or to be incorporated with it. The first part of the digestive canal is usually a simple tube—*œsophagus* (*stomodæum*)—but may be more complicated, and divided into various regions, sometimes with paired diverticula. Posteriorly it opens into the intestine. The *intestine*, constituting by far the greater part of the length of the canal, may be a simple unconstricted tube, or may be only slightly constricted at intervals by the paired gonads. In most cases the constrictions corresponding to the gonads are very deep, so that the intestine comes to be provided with two rows of lateral diverticula or cæca, which may be branched. The cæca are separated from one another by

[1] When a *tail* is present the intestine may, or may not, be continued through it.

incomplete transverse septa of dorso-ventral muscular fibres—the arrangement of the cæca and septa with the alternately arranged gonads bringing about an appearance of imperfect metamerism such as is observable in some of the Platyhelminthes (*Procerodes*, Fig. 202).

The Nemertines possess a system of vessels usually regarded as representing a **blood-vascular system** (Figs. 232 and 237), with well-defined walls consisting of a layer of epithelium surrounded by a thin layer of muscular fibres arranged circularly. There are three principal longitudinal trunks—a *median dorsal* (*dors. ves. d.b.*, *d.v.*) and two *lateral* (*lat. ves. l.v.*, *l.b.*). The blood is, in most cases, colourless, and contains rounded or elliptical, usually colourless corpuscles.

The **excretory system** has a considerable resemblance to that of the Platyhelminthes. It consists of a pair of longitudinal vessels (Fig. 232, *neph.*) which give off branches, by one or several of which each communicates with the exterior. In one species of *Baseodiscus* (*Eupolia*) there are also ducts opening into the alimentary canal. The fine terminal branches of the system are provided with *ciliary flames*, each situated in the midst of a group of cells, not in the interior of a single flame-cell as in most cases in the Flat-Worms.

There are no special **organs of respiration** in any of the group. But there is evidence that this function is carried out, in part at least, by the taking in and giving out of water through the mouth by the œsophagus.

The **nervous system** is in some respects more highly developed than in the *Turbellaria*. The *brain* (Figs. 230 and 233, *br.*, and Figs. 232, *cer. g.*, and 237, *n. g. d.*, *n. g. v.*) is composed of two pairs of ganglia,

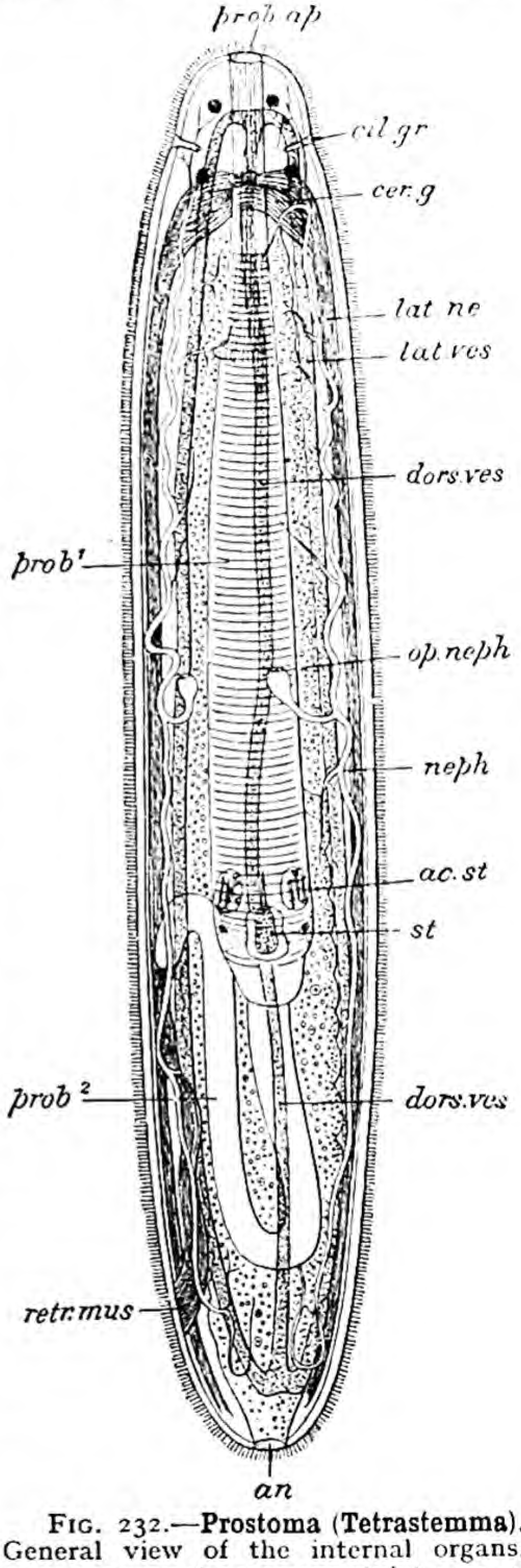


FIG. 232.—**Prostoma (Tetrastemma).** General view of the internal organs. *an.* anus; *ac. st.* accessory stylet; *cer. g.* brain; *cil. gr.* ciliated groove of cerebral organ; *dors. ves.* dorsal vessel; *lat. ne.* lateral nerve; *lat. ves.* lateral vessel; *neph.* longitudinal vessel; *op. neph.* excretory aperture; *prob*[1]. eversible part of proboscis; *prob.*[2] non-eversible part of proboscis; *prob. ap.* aperture for the protrusion of the proboscis; *retr. mus.* retractor muscle of the proboscis; *st.* stylet. (From Hatschek's *Lehrbuch.*)

dorsal and ventral, the ganglia of each pair being connected together by commissures, the dorsal situated above, the ventral below, the anterior part

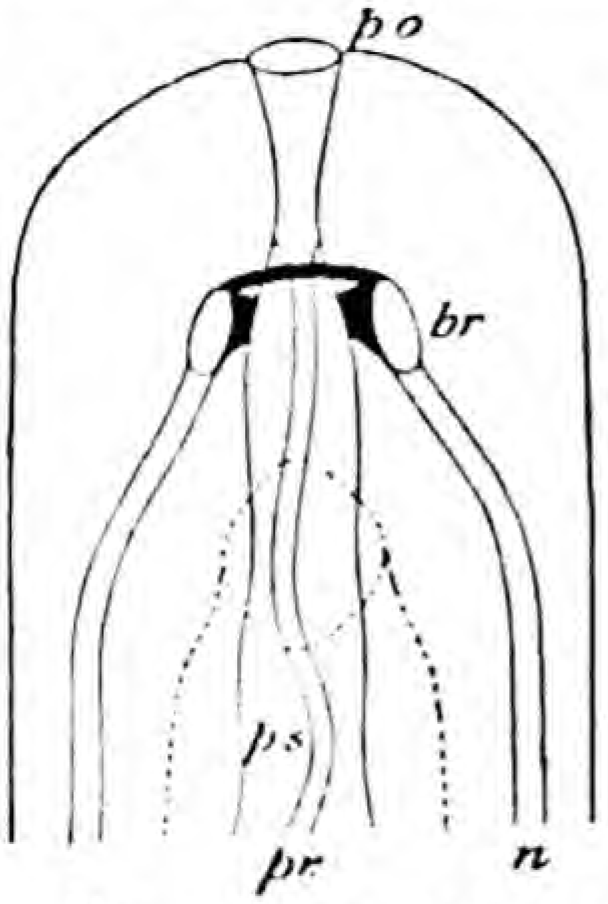
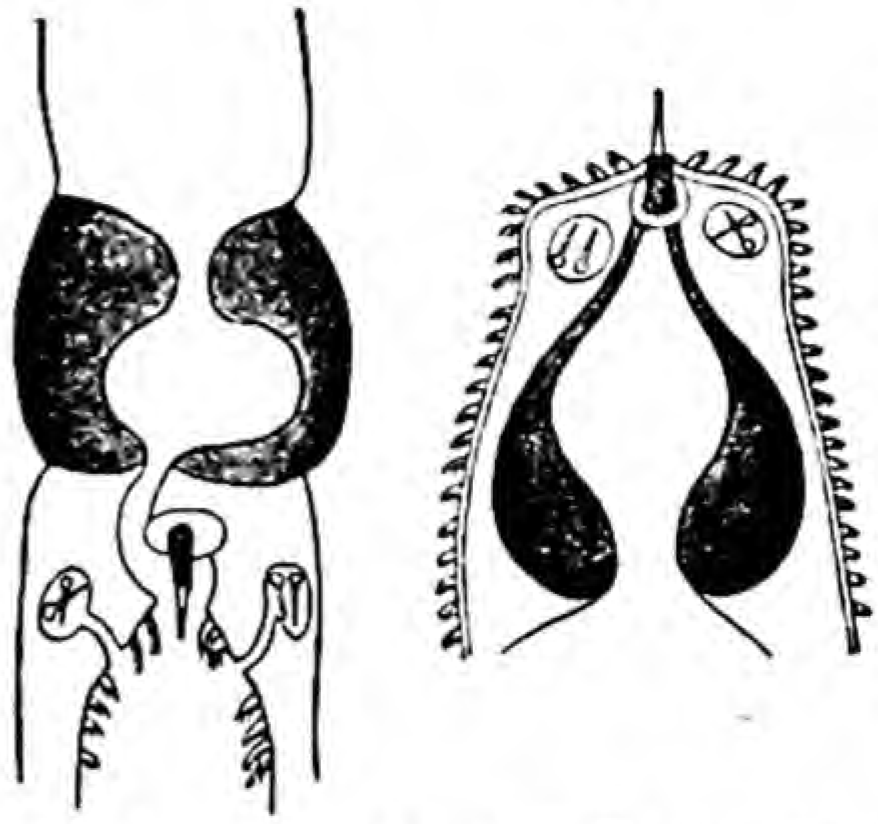


FIG. 233.—Anterior portion of the body of a Nemertine. *br.* brain-lobes; *n.* lateral nerves; *p. o.* external opening through which the proboscis is everted; *p.s.* proboscis-sheath; *pr.* proboscis. Œsophagus and mouth shown by dotted lines. (After Hubrecht.)



FIGS. 234 and 235.—Proboscis of a **Metanemertine,** with stylet reserve-sacs and muscular bulb. Fig. 234 retracted, Fig. 235 everted. (After Hubrecht.)

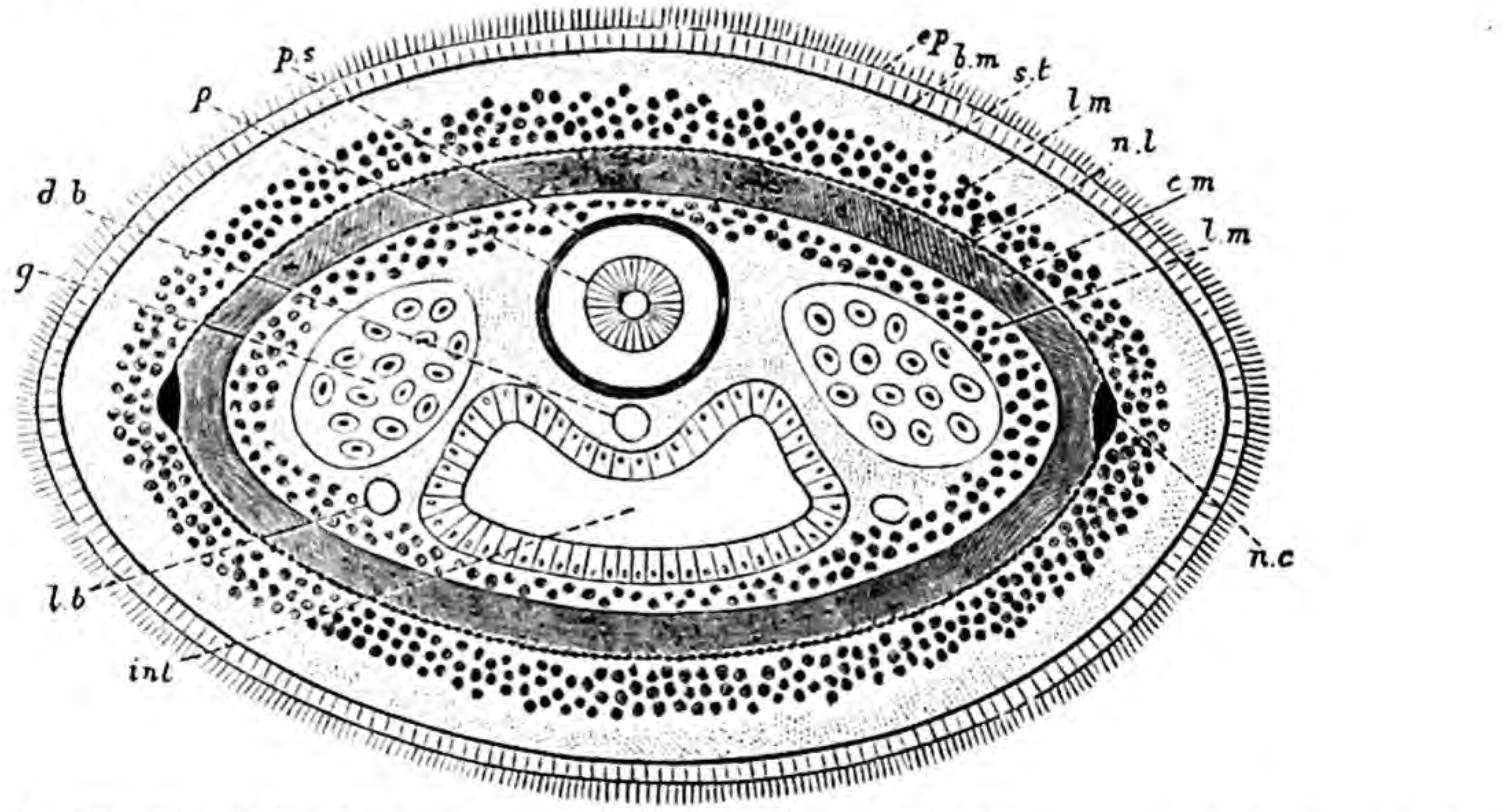


FIG. 236.—Diagrammatic transverse section of a **Nemertine** (*Heteronemertini*) through the middle region of the body. *b. m.* basement membrane; *c. m.* circular muscle layer; *d. b.* dorsal blood-vessel; *ep.* epidermis; *g.* gonads; *int.* intestine; *l. b.* lateral blood-vessel; *l. m.* longitudinal muscle layer; *n.c.* lateral nerve-cord; *n.l.* nerve-plexus; *p.* proboscis; *p. s.* proboscis sheath; *s.t.* subcutaneous layer. (After Sheldon.)

of the proboscis and proboscis sheath, and both being above the mouth and œsophagus. From the brain pass backwards a pair of thick longitudinal nerve-

cords which run throughout the length of the body. Usually these are lateral in position, sometimes approximated dorsally, sometimes ventrally. The lateral nerve-cords generally meet posteriorly in a commissure usually situated above, but in one genus below, the anus. A third median dorsal nerve of smaller size than the lateral cords extends backwards from the dorsal commissure of the brain. Associated with the nerve-cords in the *Palæonemertini* and the *Heteronemertini* is a nerve-plexus (Fig. 236, *n.l.*) extending all over the body. In the *Metanemertini*, instead of a nerve-plexus, there is a series of

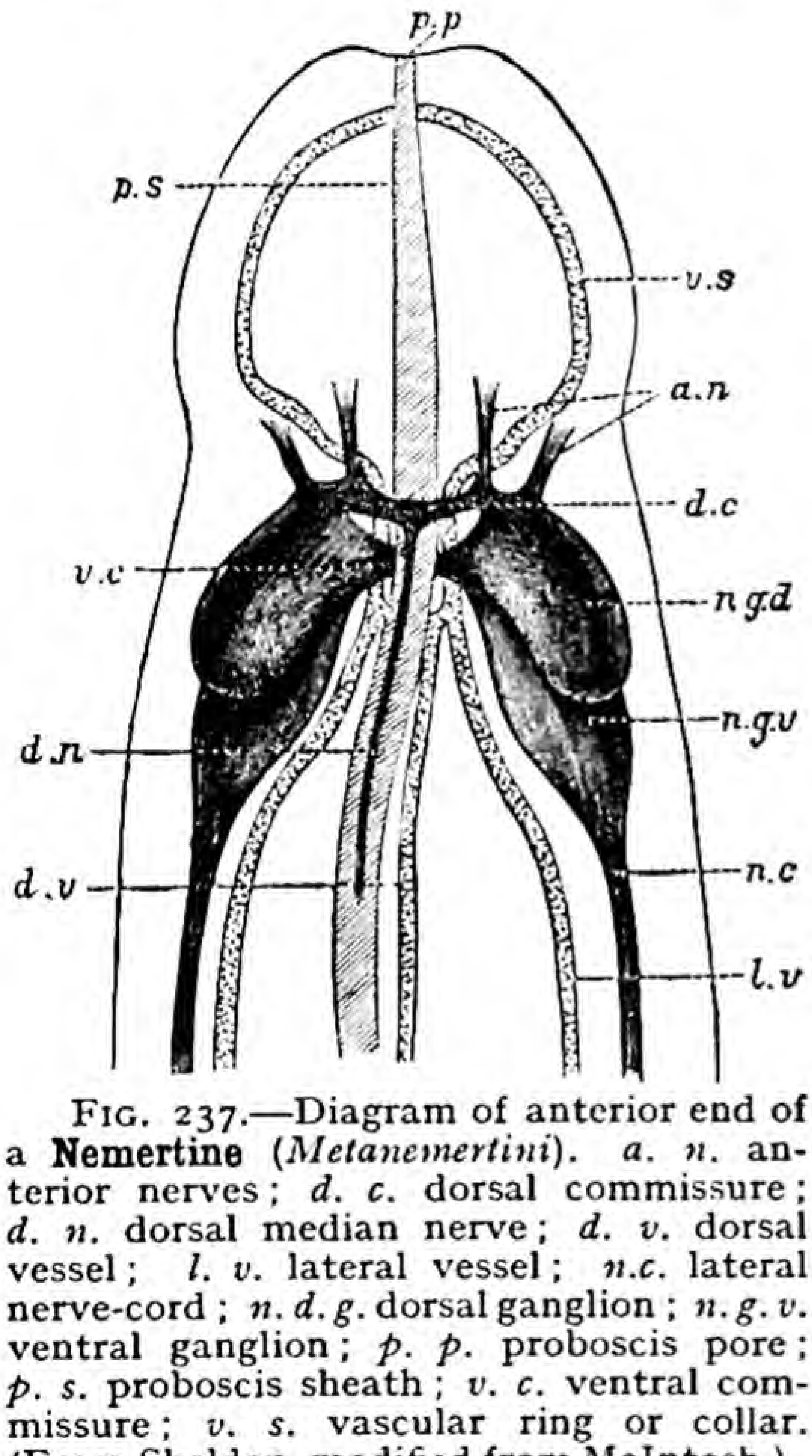


FIG. 237.—Diagram of anterior end of a **Nemertine** (*Metanemertini*). *a. n.* anterior nerves; *d. c.* dorsal commissure; *d. n.* dorsal median nerve; *d. v.* dorsal vessel; *l. v.* lateral vessel; *n.c.* lateral nerve-cord; *n. d. g.* dorsal ganglion; *n. g. v.* ventral ganglion; *p. p.* proboscis pore; *p. s.* proboscis sheath; *v. c.* ventral commissure; *v. s.* vascular ring or collar. (From Sheldon, modified from McIntosh.)

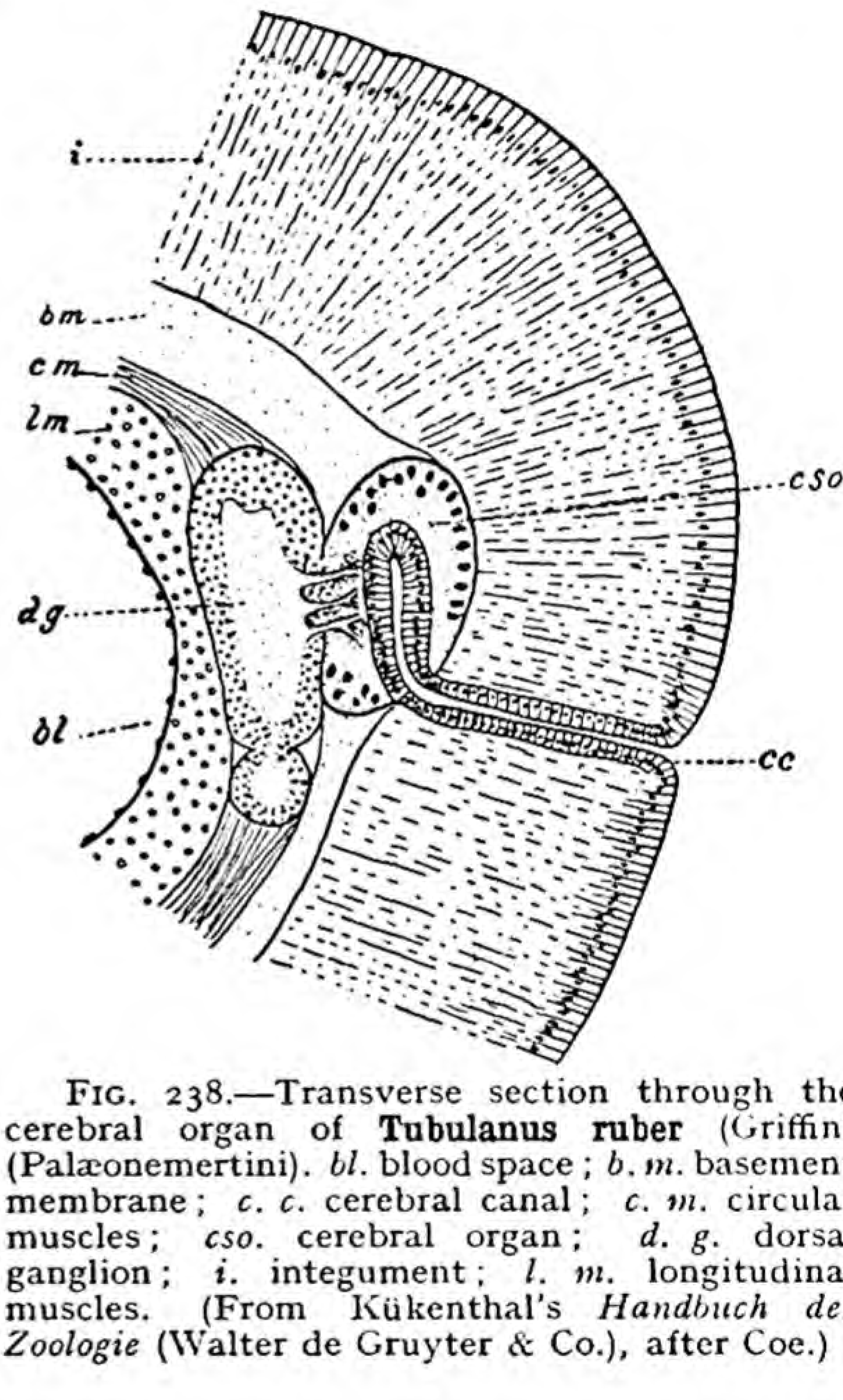


FIG. 238.—Transverse section through the cerebral organ of **Tubulanus ruber** (Griffin) (Palæonemertini). *bl.* blood space; *b. m.* basement membrane; *c. c.* cerebral canal; *c. m.* circular muscles; *cso.* cerebral organ; *d. g.* dorsal ganglion; *i.* integument; *l. m.* longitudinal muscles. (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co.), after Coe.)

slender transverse connectives running across at short intervals between the lateral nerve-cords, and from each cord are given off numerous branches arranged with some regularity.

The position of the brain and lateral nerve-cords and the nerve-plexus, or the system of commissures and nerve-branches, varies in the different groups. In part of the Palæonemertini they occupy the most primitive position, being quite superficially situated at the bases of the epidermal cells. In the rest they are deeper; in the Metanemertini they lie in the parenchyma within the

muscular layers. The median cord is always, except in the Heteronemertines, superficially placed.

A remarkable apparatus connected with the nervous system is that composed of a pair of peculiar structures known as the **cerebral organs**. When most highly developed these consist of a pair of ciliated tubes, opening externally in the region of the brain and terminating internally in close relation to the dorsal ganglion of the brain or a special ganglion distinct from the latter. The external aperture may be situated in a groove or furrow (Fig. 232, *cil. gr.*), vertical or horizontal, of varying extent. This apparatus which was formerly described as having a respiratory function is in all probability an organ of the *chemical sense*. It has some resemblance to the ciliated pits developed in certain Turbellaria (Fig. 238).

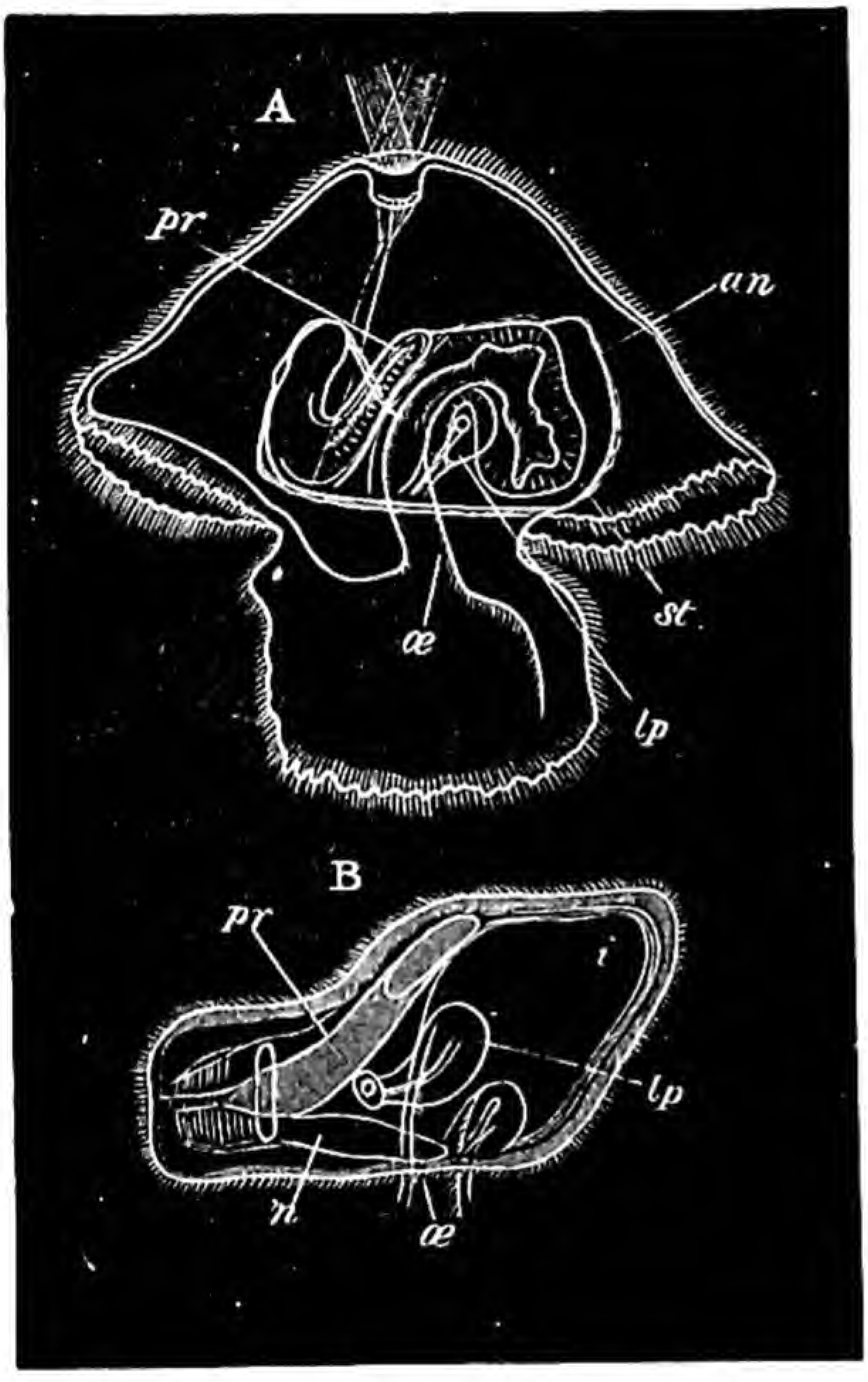


FIG. 239.—*A*, Pilidium with advanced Nemertine worm; *B*, ripe embryo of Nemertes from interior of pilidium. *an.* amnion, or investment of the embryo; *i.* intestine; *l. p.* lateral pit; *n.* nervous system; *œ.* gullet; *pr.* proboscis; *st.* stomach. (From Balfour, after Bütschli.)

Eyes are present in the majority of Nemertines, and in the more highly organized species occur in considerable numbers. Sometimes they are of extremely simple structure; in other cases they are more highly developed, having a spherical refractive body with a cellular "vitreous body," and a "retina" consisting of a layer of rods enclosed in a sheath of dark pigment, each rod having a separate nerve-branch connected with it. **Statocysts** containing statoliths have been found in only a few of the Nemertines.

Reproductive System.—Most species are *diœcious*. The *ovaries* (Fig. 230, *ov.*) and *testes* are situated in the intervals between the intestinal cæca. The ovary or testis is a sac lined by cells which give rise to ova or spermatozoa; when these are mature each sac opens by means of a narrow duct leading to the dorsal, rarely to the ventral, surface, on which it opens by a pore.

Development.—Some of the Nemertines go through a metamorphosis; in the others the development is direct. The characteristic larval form is the *pilidium* (Fig. 239). This is a helmet-shaped body with side lobes like ear-

lappets, and a bunch of cilia representing a spike. In the metamorphosis a number of ectodermal invaginations, growing inwards around the intestine, fuse together and form the integument and body-wall of the future worm, which subsequently frees itself from its investment and develops into the adult form. In others there is a ciliated creeping larva called the "*larva of Desor,*" in the interior of which the larval worm is developed much as in the case of the pilidium.

Distinctive Characters and Classification.

The Nemertini are ciliated, unsegmented worms with elongated body, without distinct cœlome. There is an eversible proboscis enclosed in a sheath and capable of being protruded to a great length through an aperture situated usually in front of and above the mouth. The intestine usually has distinct lateral diverticula, and there is a posteriorly situated anus. There is a blood-vascular system, and also a system of excretory vessels with ciliary flames.

Sub-Class I.—Anopla.

Nemertini in which the mouth is situated behind the brain. Proboscis without stylets.

Order 1.—Palæonemertini.

Dimyarian Nemertines with the lateral nerve-cords situated outside or within the muscular layers. The mouth is situated behind the brain. The proboscis is devoid of stylet.

Order 2.—Heteronemertini.

Trimyarian Nemertines, in which the lateral nerve-cords are in the muscle-layers, between the outer longitudinal and the circular layers. The mouth is situated behind the brain. The proboscis has no stylet.

Example: *Baseodiscus* (*Eupolia*).

Sub-Class II.—Enopla.

Nemertini in which the mouth is situated in front of or under the brain. Proboscis generally with stylets.

Order 1.—Metanemertini.

Dimyarian Nemertines, in which the lateral nerve-cords lie inside the muscular layers in the parenchyma. The mouth is situated in front of the brain. The proboscis is generally provided with stylets. A ventral (stomodæal) cæcum is present.

Examples: *Drepanophorus; Prostoma* (*Tetrastemma*), Fig. 232.

The Nemertines are almost exclusively marine; and the greater number live between tide-marks or at moderate depths; a few have been obtained from considerable depths. The comparatively small number of terrestrial and

fresh-water forms are all *Metanemertini*. The Nemertines progress for the most part by slow crawling movements, leaving a track of slime behind them. Some burrow freely in mud or sand, the proboscis being made use of to help in the process. Some are able to swim by means of undulating movements of the body. Nearly all are carnivorous, and either capture living prey in the shape of small invertebrates of various kinds, or feed on dead fragments. The chief function of the proboscis is the capture of living prey, around which it becomes coiled and then draws the prey towards the mouth. One Nemertine lives in the interior of a Crustacean, and is probably a true parasite. Others live, apparently as commensals in the pharynx or atrial cavity of Ascidians, or within the mantle cavity of bivalve Mollusca.

A striking feature of the Nemertines is the readiness with which, on being irritated by handling or by the action of some chemical agent, they break up transversely into fragments. This takes place most freely when the body is highly charged with sexual products, but is by no means confined to that condition. The process probably takes place spontaneously under certain circumstances. The broken-off fragments may remain alive for a considerable time, and under suitable conditions regeneration of the lost parts is readily effected, so that it is possible to look upon the entire process as a form of asexual reproduction.

SECTION VI

In this section five classes of *non-cœlomate* animals: the *Nematoda*, *Nematomorpha*, *Acanthocephala*, *Rotifera*, and *Calyssozoa* (*Endoprocta*) will be described. Their affinities and phylogenetic position are still very obscure. That they are dealt with in a common section is entirely a matter of convenience.

THE NEMATODA.

The Nematoda or Round-worms are elongated, cylindrical, worm-like animals, many genera of which are extremely abundant in fresh and salt water, as well as in the soil. The best-known forms, however, are internal parasites in animals or plants.

1. Example of the Class—The Common Round-worm of Man. (*Ascaris lumbricoides.*)

Ascaris lumbricoides is a common parasite in the human intestine: a closely allied if not identical form (*A. suilla*) occurs in the Pig, and another (*A. megalocephala*) in the Horse. The following description will apply to any of these. The female *A. lumbricoides* is about 20–40 cm. (8–16 in.) long, and about 6–8 mm. (¼ in.) in diameter; the male is considerably smaller.

External Characters.—When fresh, the animal is of a light yellowish-brown colour: it is marked with four longitudinal streaks, two of which, very narrow

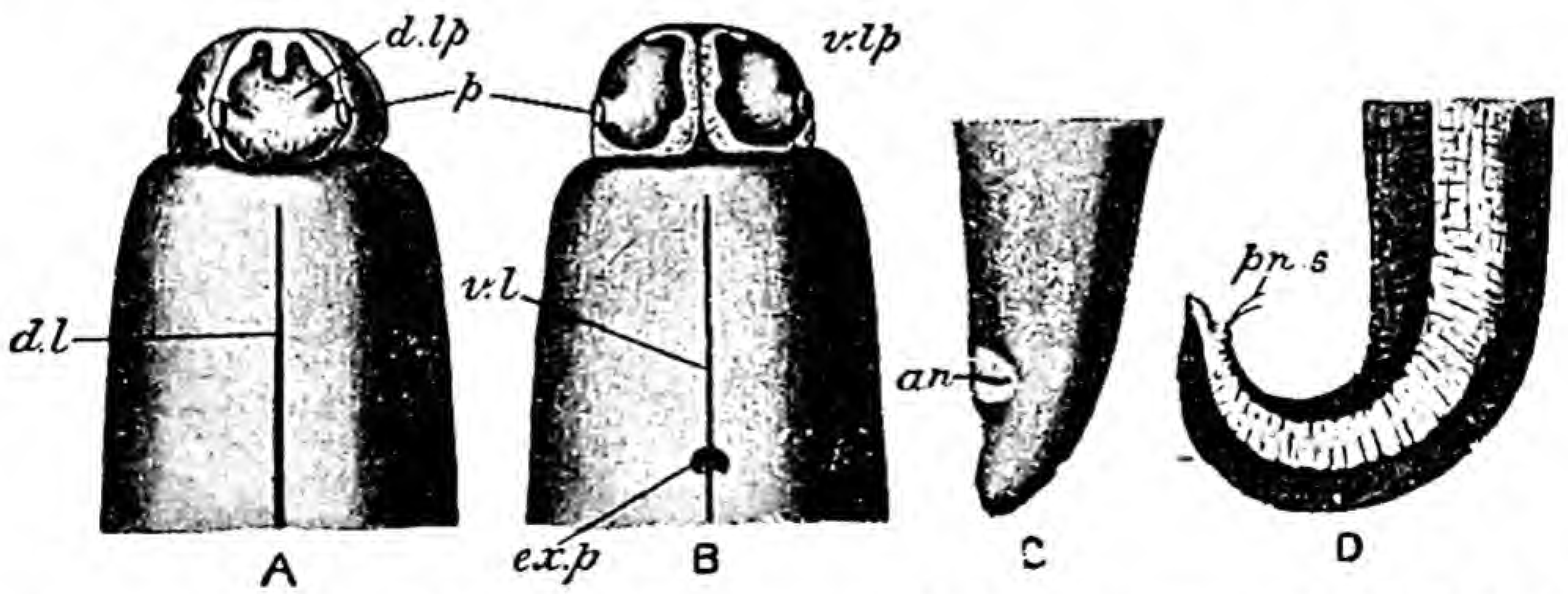


Fig. 240.—**Ascaris lumbricoides.** *A*, anterior end from above; *B*, the same from below; *C*, posterior end of female, *D*, of male, side view. *an.* anus; *d. lp.* dorsal lip; *d. l.* dorsal line; *ex. p.* excretory pore; *p.* papillæ; *pn. s.* penial setæ; *v. l.* ventral line; *v. lp.* ventral lip. (After Leuckart.)

and pure white in the living worm, are respectively dorsal and ventral in position, and are called the *dorsal* and *ventral lines* (Fig. 240, *d. l.*, *v. l.*): the other

two are lateral in position, thicker than the former, and brown in colour, and are distinguished as the *lateral lines*. The *mouth* is anterior and terminal in position, and is bounded by three lobes, or *lips*, one median and dorsal (*d. lp.*), the other two ventro-lateral (*v. lp.*). A very minute aperture on the ventral side, and about 2 mm. from the anterior end, is the *excretory pore* (*ex. p.*). At about the same distance from the pointed and down-turned posterior end is a transverse aperture with thickened lips, the *anus* (*an.*), which in the male serves also as a reproductive aperture and gives exit to a pair of needle-like chitinoid bodies, the *penial setæ* (*pn. s.*). In the female the reproductive aperture or

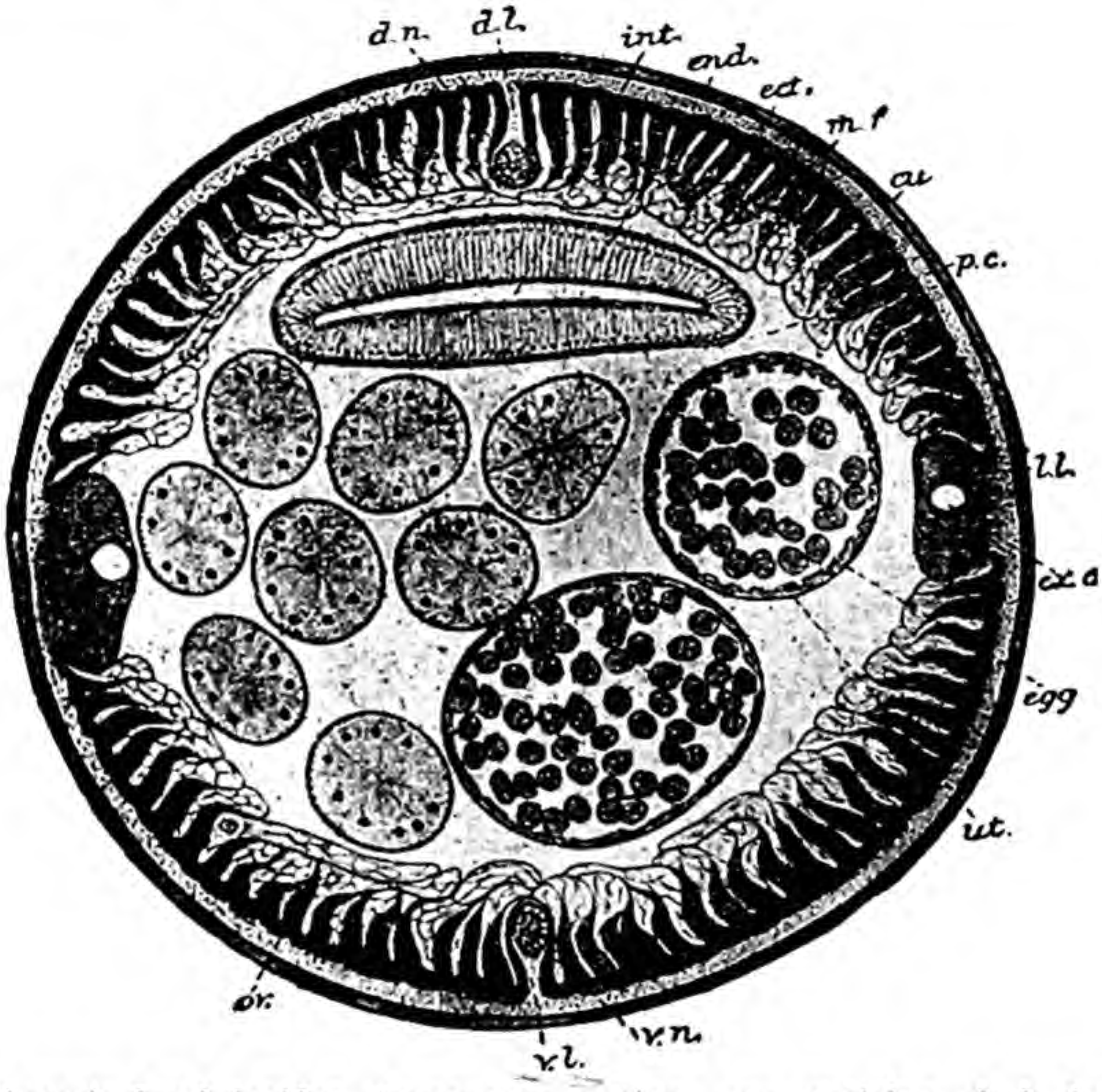


FIG. 241.—**Ascaris lumbricoides,** transverse section. *cu.* cuticle; *d. l.* dorsal line; *d. n.* dorsal nerve; *ect.* ectoderm; *egg.* egg; *end.* endoderm; *ex. c.* excretory canal; *int.* intestine; *l. l.* lateral line; *m. f.* muscle fibre; *ov.* ovary; *p. c.* perivisceral cavity; *ut.* uterus; *v. l.* ventral line; *v. n.* ventral nerve. (From Borradaile's *Manual of Elementary Zoology* (Oxford University Press).)

gonopore is separate from the anus, and is situated on the ventral surface about one-third of the length of the body from the anterior end (Fig. 243, *gnp.*). The sexes are also distinguished externally by the form of the short *tail*, or post-anal portion of the body, which in the male is sharply curved downwards (Fig. 240, *D*), while in the female (*C*) its ventral contour is nearly straight.

Body-wall.—The outer surface of the body is furnished by a delicate, transparent, elastic membrane, of a firm material of albuminoid composition, the *cuticle* (Fig. 241, *cu.*). It is divisible into several layers containing a system of fine vertical channels (*A. megalocephala*), and is wrinkled transversely, so as to

give the animal a segmented appearance. Beneath the cuticle is a protoplasmic layer containing scattered nuclei and longitudinal fibres, and representing a *syncytial ectoderm—i.e.*, an ectoderm in which the cell-boundaries are not differentiated, and whose cellular nature is recognizable only by the nuclei. The cuticle is, as usual, a secretion of the ectoderm.

Beneath the ectoderm is a single layer of *muscular fibres* (*m.f.*), arranged longitudinally, and bounding the body-cavity. The structure of the muscles is very peculiar: each (Fig. 242, *A*) has the form of a spindle, striated longitudinally, and produced on its inner face, (*i.e.*, towards the body-cavity) into a large and almost bladder-like mass of protoplasm (*p.*) containing a nucleus (*nu.*). Apparently the whole of this structure is derived from a single cell, part of which has become differentiated into contractile substance (*c.*), the rest remaining protoplasmic. In transverse section the contractile portion (*B*, *c.*) has the form of a plate bent upon itself so as to be, as it were, wrapped round the protoplasmic portion (*p.*). The protoplasmic processes project to a greater or less extent into the body-cavity, sometimes practically obliterating it, and are produced into delicate filaments (*f.*) which take a transverse direction, and are mostly inserted into the dorsal and ventral lines.

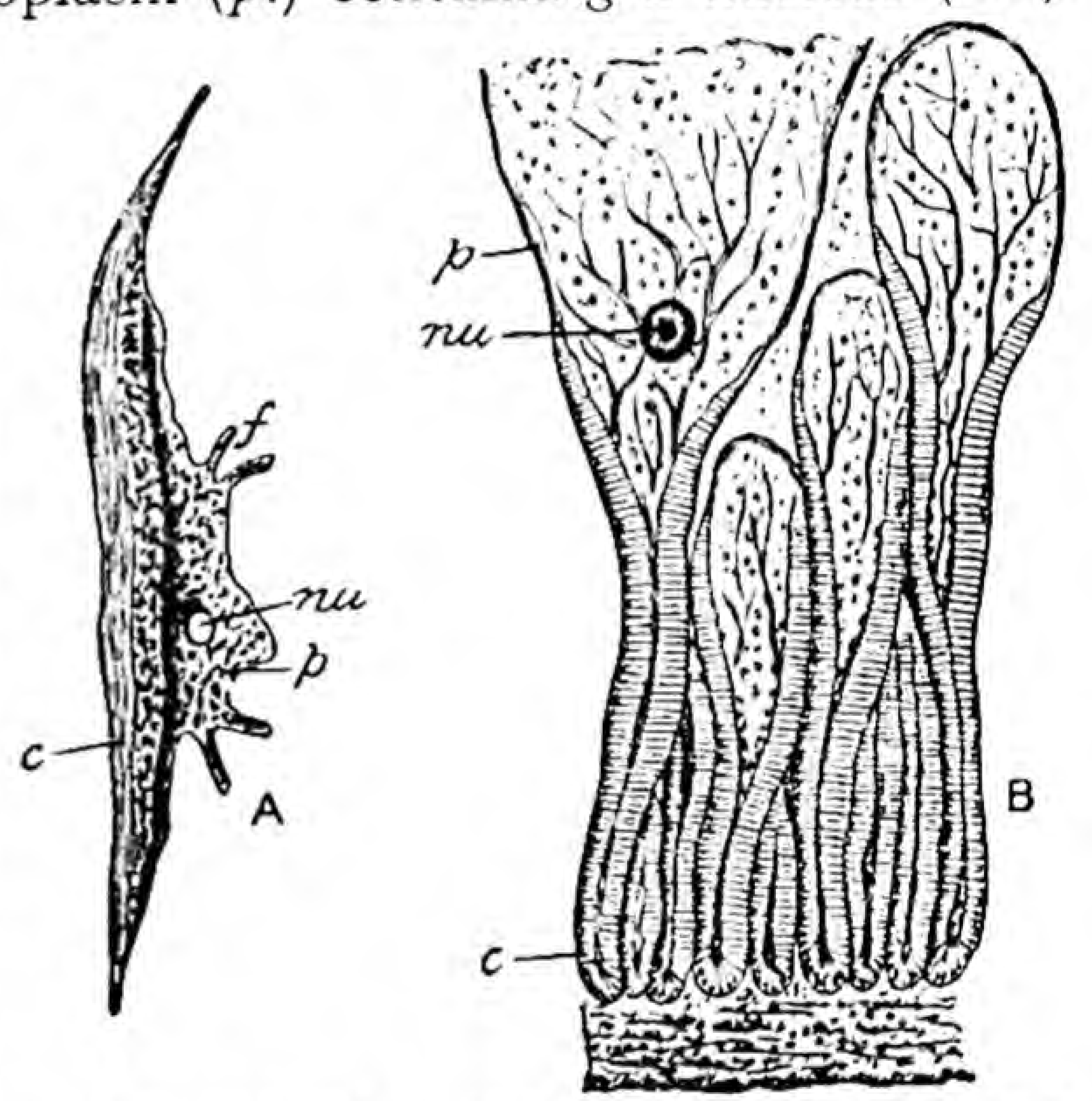


FIG. 242.—**Ascaris lumbricoides.** *A*, a single muscle fibre; *B*, several fibres in transverse section with portion of ectoderm (below). *c.* contractile substance; *f.* fibrous processes; *nu.* nucleus; *p.* protoplasmic portion. (After Leuckart.)

The muscular layer is not continuous, but is divided into four longitudinal bands or quadrants, two dorso-lateral and two ventro-lateral, owing to the fact that at the dorsal, ventral, and lateral lines the ectoderm undergoes a great thickening and projects inwards, between the muscles, in the form of four longitudinal ridges (Fig. 241, *d. l.*, *v. l.*, *l. l.*). The ridges are composed of fibres continuous with the fibres of the ectoderm. It is this arrangement that gives rise to the lines seen externally. The ridges forming the lateral lines are much more prominent than the other two.

Digestive Organs.—The mouth leads into the anterior division of the enteric canal, the *œsophagus* the posterior part of which is called *pharynx* (Fig. 243, *ph.*): its walls are very muscular, its cavity is three-rayed in cross-section, and it is lined by a cuticle secreted from the epithelial layer and continuous, at the mouth, with that of the body-wall. Posteriorly the pharynx

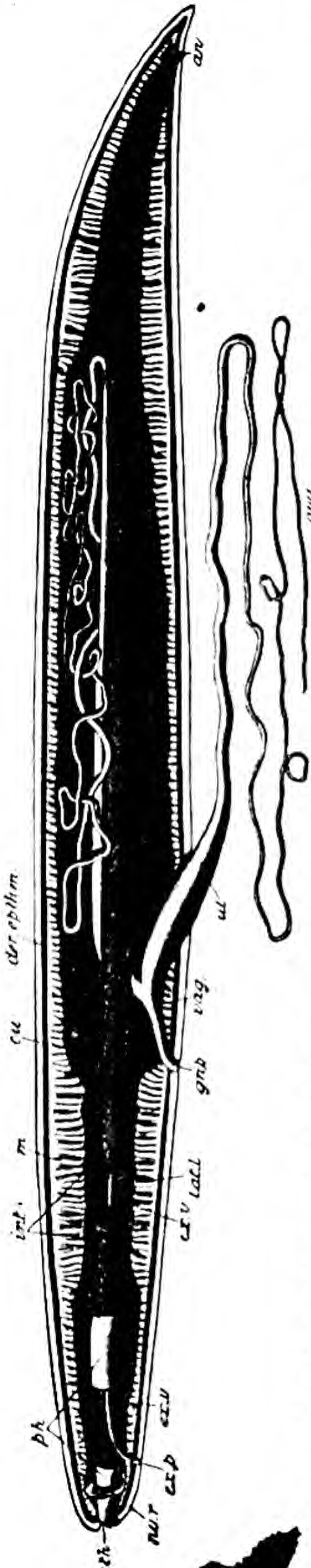


FIG. 243.—**Ascaris lumbricoides.** Semi-diagrammatic dissection of the female. *an.* anus; *cu.* cuticle; *der. epthm.* deric epithelium; *ex. p.* excretory pore; *ex. v.* excretory vessel; *gnp.* gonopore; *int.* intestine, partly cut away; *lat. l.* lateral line; *m.* muscular layer; *mth.* mouth; *nv.r.* nerve-ring; *ovy.* ovary, that of the right side in situ, the left spread out; *ph.* pharynx, partly cut away; *ut.* uterus; *vag.* vagina.

opens into the *intestine* (*int.*), a thin-walled tube, flattened from above downwards, and formed of a layer of epithelial cells bounded both internally and externally by a delicate cuticle: it has no muscular layer (Fig. 241, *int.*). Posteriorly the intestine narrows considerably to form the short *rectum*, which has a few muscular fibres in its walls and opens externally by the anus (Fig. 243, *an.*). The food, consisting of the semi-fluid contents of the intestine of the host, is sucked in by movements of the œsophagus, and is then absorbed into the system through the walls of the intestine. The food being already digested by the host, there is no need of digestive gland cells, such as occur in animals which prepare their own food for absorption.

The epithelial lining of the œsophagus and pharynx are derived from the ectoderm, being formed as an inturned portion of the outer layer of the bodywall. The epithelium of the intestine, on the other hand, is endodermal, this portion of the canal being derived from the archenteron of the embryo.

Between the enteric canals and the body-wall is a distinct space, the **body-cavity**, containing a clear fluid and more or less encroached upon by the protoplasmic processes of the muscle-cells. The cavity is bounded externally by these processes, internally by the outer cuticle of the intestine: there is no trace of epithelial lining such as occurs in most of the higher animals, but the space is occupied by a very small number of so-called giant cells, the cytoplasm of which is greatly vacuolated. In other Nematodes connective tissue-cells have been found in the body-cavity. The body-cavity of the Nematode, in fact, does not exactly correspond to the cœlome to be met with in most higher phyla. It is not to be derived, directly or indirectly, from the archenteron of the

embryo, and it does not lie, like a true cœlome, between layers of the mesoderm.

The **excretory system** consists of two longitudinal canals (*ex. v.*), one in each lateral line. Anteriorly these pass to the ventral surface, unite with one another, and open by the minute excretory pore (*ex. p.*) already noticed. The system is not ciliated, contains no flame-cells, and has no internal openings. Each canal is an excavation in a single enormously elongated cell with a single nucleus. Generally in close contact with the excretory canals are found four or six big, tuft-shaped cells with ramifying processes, which are capable of taking up solid waste matter from the body-cavity. It is said that this waste matter is not only stored there, but handed on in the dissolved state to the excretory canals.

The **nervous system** consists of a ring (*nv. r.*) surrounding the pharynx and giving off six nerves forwards and six backwards (Fig. 244). Of the latter two are of considerable size, and run in the dorsal and ventral lines respectively (*dln.*, *vln.*). They are connected with one another by transverse commissures (*c.*), and the ventral nerve swells into a ganglion just in front of the anus. The pharyngeal nerve-ring contains nerve-cells, and its ventral portion (*un.*) is thickened and ganglion-like. The only sense-organs are little elevations, the *sensory papillæ* (Fig. 240, *p.*), on the lips.

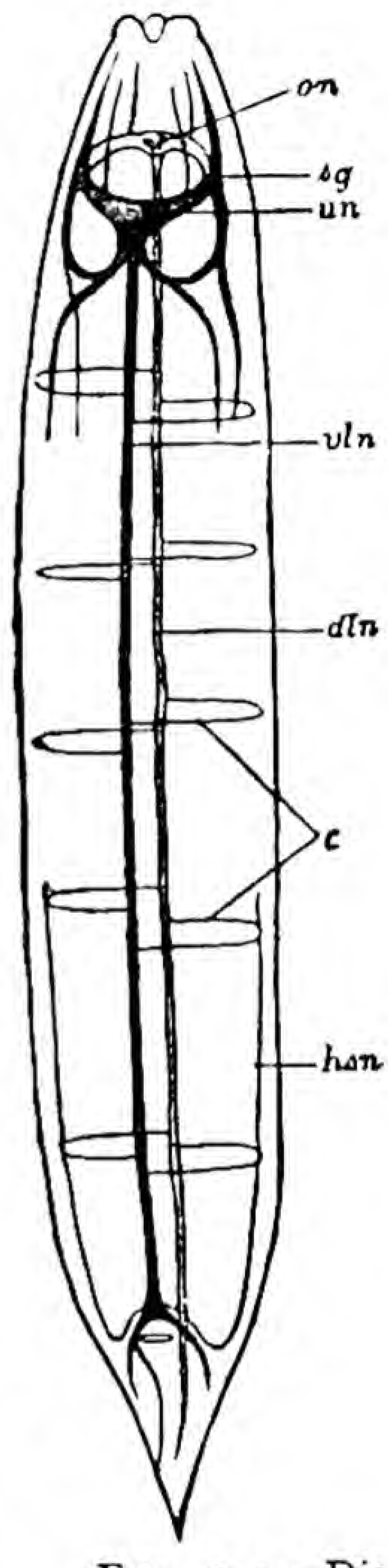


FIG. 244.—Diagram of nervous system of **Nematoda.** *c.* commissures; *dln.* dorsal nerve; *hsn.* posterior lateral nerve; *on.* upper and *un.* under portion of nerve-ring; *sg.* lateral swellings; *vln.* ventral nerve. (From Lang, after Bütschli.)

The **reproductive organs** are formed on a peculiar and very characteristic pattern. The *testis* (Fig. 245, *ts.*) is a long, coiled thread, about the thickness of fine sewing-cotton, and occupying a considerable portion of the body-cavity. At its posterior end it is continuous with the *vas deferens*, the two passing insensibly into one another so that the junction is not visible externally. The vas deferens, in its turn, becomes continuous with a wide canal, the *vesicula seminalis* (*vs. sem.*) which opens by a short, narrow muscular tube, the *ductus ejaculatorius*, into the rectum. Behind the rectum, and opening into its dorsal wall, are paired muscular sacs (*s.*), containing the *penial setæ* (*pn. s.*) already noticed. The anterior end of the testis consists of a solid mass of sex-cells; passing backwards there is found a cord or *rachis* occupying the axis of the tube and having the sperm-cells attached to it; still further back the sperms become gradually differentiated, and are finally set free in the vas

deferens. The sperms are peculiar rounded cells (Fig. 24, *c. d. e.*); when transferred into the body of the female they exhibit amœboid movements, but as long as they remain in the male ducts they are non-motile: they have no trace at any stage of the characteristic tail of the typical sperm. In this connection it may be mentioned that the tissues of Ascaris are remarkable for the total *absence of cilia.*

The organs of the female (Fig. 243) resemble those of the male, but are double instead of single. There are two coiled, thread-like ovaries (*ovy.*), each passing insensibly into a uterus (*ut.*). In the ovary, as in the testis, the eggs are developed in connection with an axial cord or rachis. The two uteri unite in a short muscular vagina (*vag.*) which opens, as already

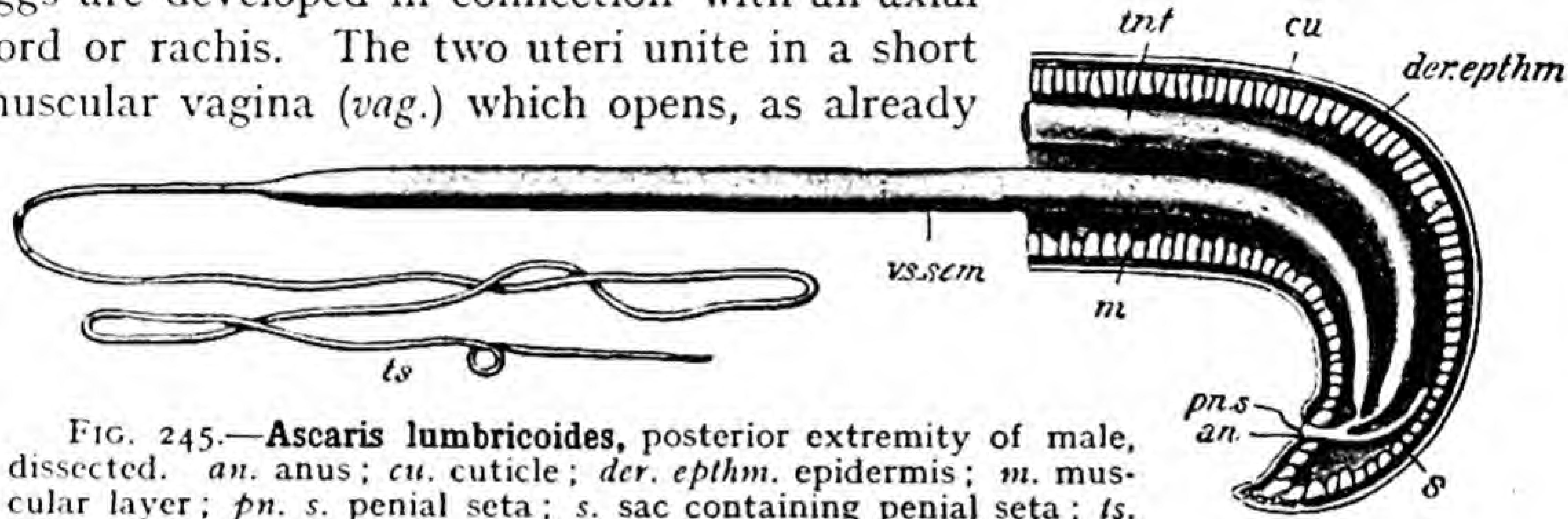


FIG. 245.—**Ascaris lumbricoides,** posterior extremity of male, dissected. *an.* anus; *cu.* cuticle; *der. epthm.* epidermis; *m.* muscular layer; *pn. s.* penial seta; *s.* sac containing penial seta; *ts.* testis; *vs. sem.* vesicula seminalis.

seen, on the ventral surface of the body (*gnp.*) at about one-third of the entire length from the head.

Development.—The eggs are produced in immense numbers—at the rate, it has been reckoned, of about 15,000 a day. They are fertilized in the upper part of the uterus, each becoming enclosed in a chitinoid egg-shell, and are passed out of the body of the host with its fæces. The infection is direct, without intermediate host, the embryo-containing eggs being taken, in water, or in soil accidentally swallowed, into the intestine of a new human host, in which the embryos, escaping from the eggs, become mature.

2. General Organization.

External Characters.—The Nematoda vary much in size: the little *Anguillula*, one of the commonest of aquatic animals, does not exceed 1 mm. in length, while the dreaded parasite known as the Guinea-worm (*Filaria medinensis*) is sometimes as much as 2 metres (6 ft.) long. The length is always great in proportion to the diameter, and the body is always bluntly pointed at the anterior end and either pointed or forked posteriorly.

Body-wall.—The body is always covered by a cuticle secreted by the deric epithelium or external ectoderm (*sub-cuticle*). The cuticle is usually smooth, sometimes beset with spines or hooks, sometimes ringed. In certain species it is raised up to form a pair of lateral fin-like folds running along the

sides of the body for some distance. A regular ecdysis or moulting of the cuticle at intervals takes place in many Nematodes. The sub-cuticle takes the form of a protoplasmic layer with scattered nuclei. Beneath the ectoderm is a muscular layer, which in many genera has the same structure as in Ascaris, *i.e.*, consists of a single layer of longitudinal fibres, interrupted at the dorsal, ventral, and lateral lines, each fibre being spindle-shaped and produced into a protoplasmic process which projects into the body-cavity. But in many forms (*e.g.*, *Strongylus*) the muscle-cells are flat rhomboidal plates (Fig. 246), and each quadrant contains only two rows, the total number in a transverse section being therefore eight.

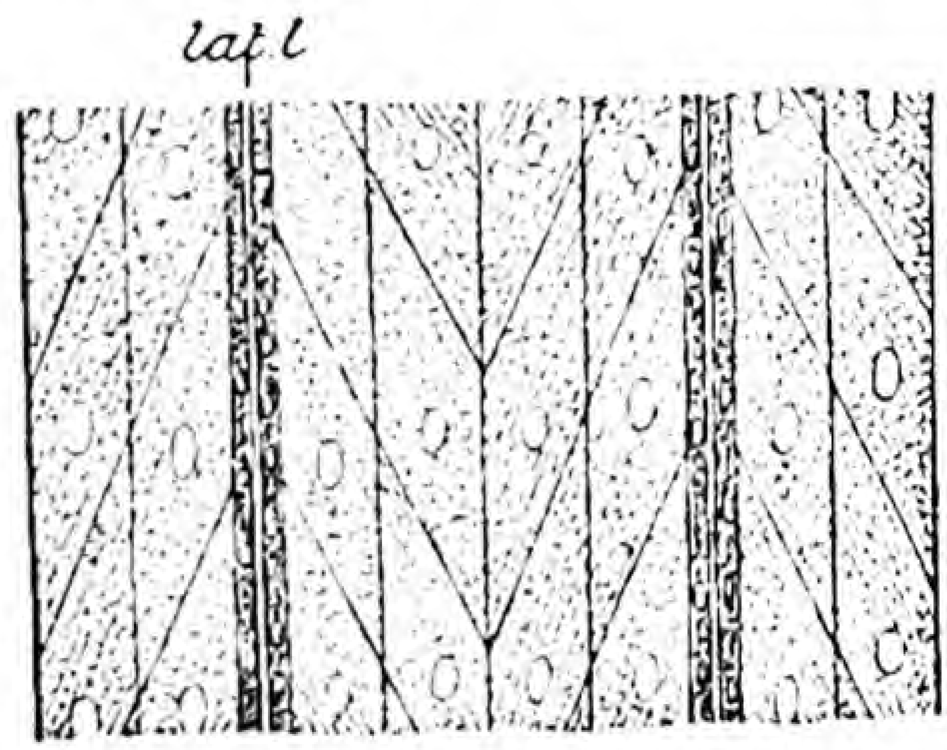


FIG. 246.—The body-wall of a platymyarian **Nematode,** spread out. *lat. l.* lateral lines. (After Leuckart.)

Enteric Canal.—The mouth is frequently armed with spines (Fig. 247, *C*), by means of which the worms draw blood from the intestinal blood-vessels of their host. Many free-living forms have a sharp stylet for piercing the tissues of the plants on which they feed, and a suctorial apparatus for absorbing the juices. The posterior end of the œsophagus is often dilated to form a globular chamber with muscular walls, the gizzard (Fig. 248, *gz.*). The alimentary canal in some rare cases has hollow appendages in the form of œsophageal glands or intestinal cæca. In Ancylostoma a pair of pear-shaped bodies of

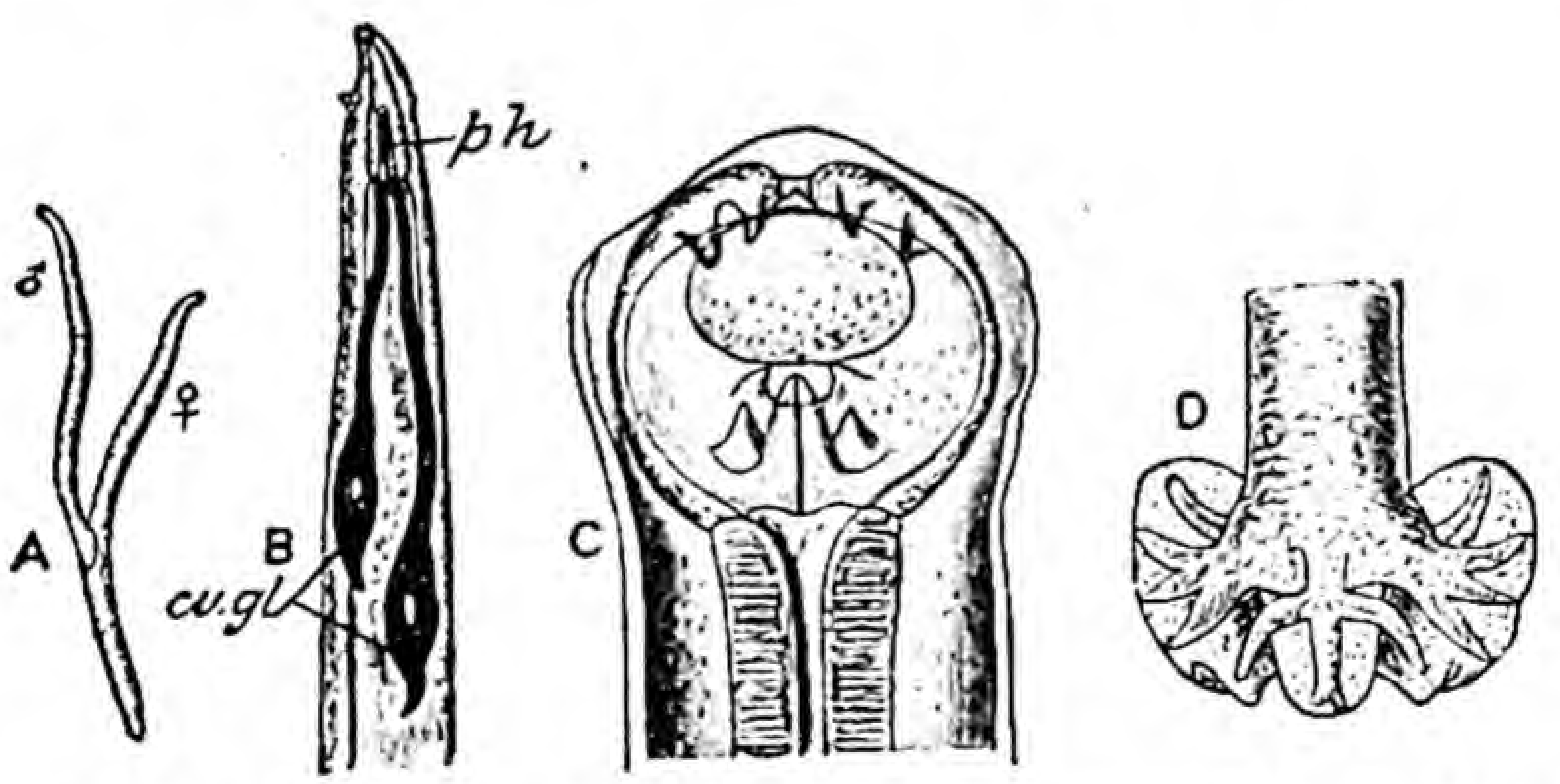


FIG. 247.—**Ancylostoma duodenale.** *A*, male and female *in coitu*. *B*, anterior end, showing: *cv. gl.* cervical glands; *ph.* pharynx. *C*, mouth with spines; *D*, posterior end of male, with bursa. (After Leuckart.)

unknown function, the so-called *cervical glands* (Fig. 247, *B*, *cv. gl.*), lie one on each side of the pharynx.

When definite **excretory organs** exist, they take the form of narrow longitudinal canals similar to those described as occuring in *Ascaris*—each canal being an excavation in a single enormously elongated cell, and the system

having a median ventral opening. Sometimes only one of the canals is developed. Flame-cells are never present.

The **nervous system** has the structure already described in Ascaris.

The **reproductive organs** in all the Nematoda resemble those of Ascaris, the only important variation depending upon the fact that in the smaller forms the entire genital tube (gonad *plus* gonoduct) is short and not coiled (Fig. 248, *ts.* and *v. df.*). A few forms are hermaphrodite, but, instead of having a double set of reproductive organs, as in Platyhelminthes, organs of the ordinary female nematode-type are present, and the gonads produce first sperms and afterwards ova. Such animals are said to be *protandrous* (male products ripen first), and self-fertilization is as effectually prevented as if the organs of the two sexes were distinct.

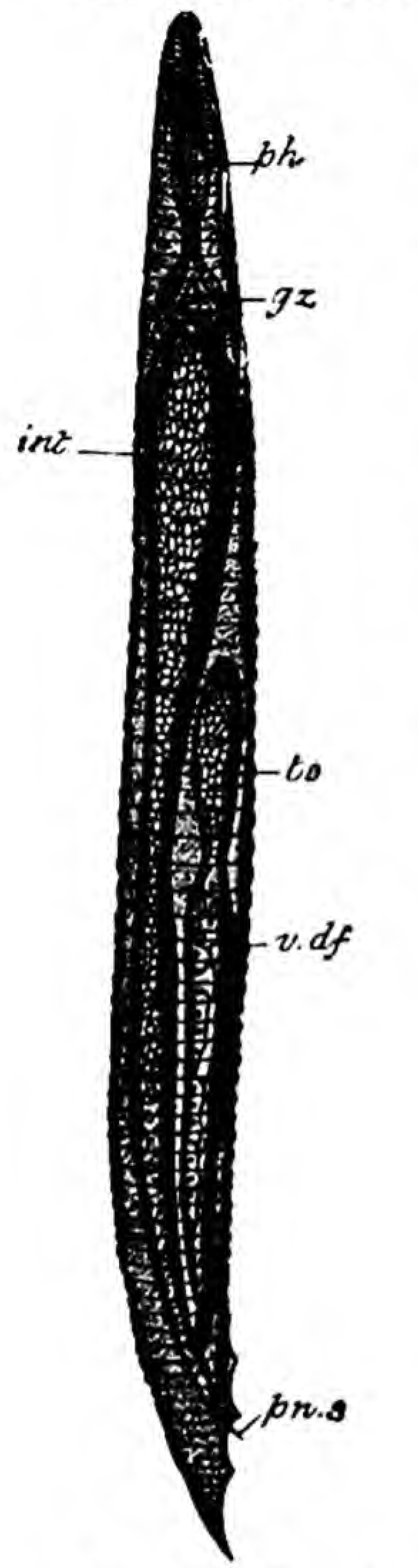


FIG. 248.—**Oxyuris**, from the right side. *gz.* gizzard; *int.* intestine; *ph.* pharynx; *pn. s.* penial setæ; *ts.* testis; *v. df.* vas deferens. (From Shipley, after Galeb.)

The **development** of Nematodes begins in some cases only after the eggs have been laid: such eggs are almost always provided with thick shells. In other cases the earlier stages, and sometimes even considerably more advanced stages, are passed through in the uterus of the mother, and a few (*Trichinella spiralis*, species of *Ascaris*, species of *Filaria* and others) are viviparous. In Ascaris the ovum divides first into a dorsal and a ventral cell (Fig. 249, AB and P_1). AB becomes subdivided into an anterior and posterior cell (Fig. 250 A, A and B) and P_1 into an upper cell $EMST$ and a lower cell P_2. The four-celled embryo is now T-shaped. The two ventral cells $EMST$ and P_2 change their position, $EMST$ coming to lie in front of P_2 (Fig. 250 B). At the next cleavage both A and B divide into right and left cells (Fig. 250 C) and the two ventral cells $EMST$ and P_2 divide into MST, E, P_3, and C, forming a median row of four cells. The descendants of cell AB undergo repeated division to form a layer of ectoderm cells. MST gives rise to meso-

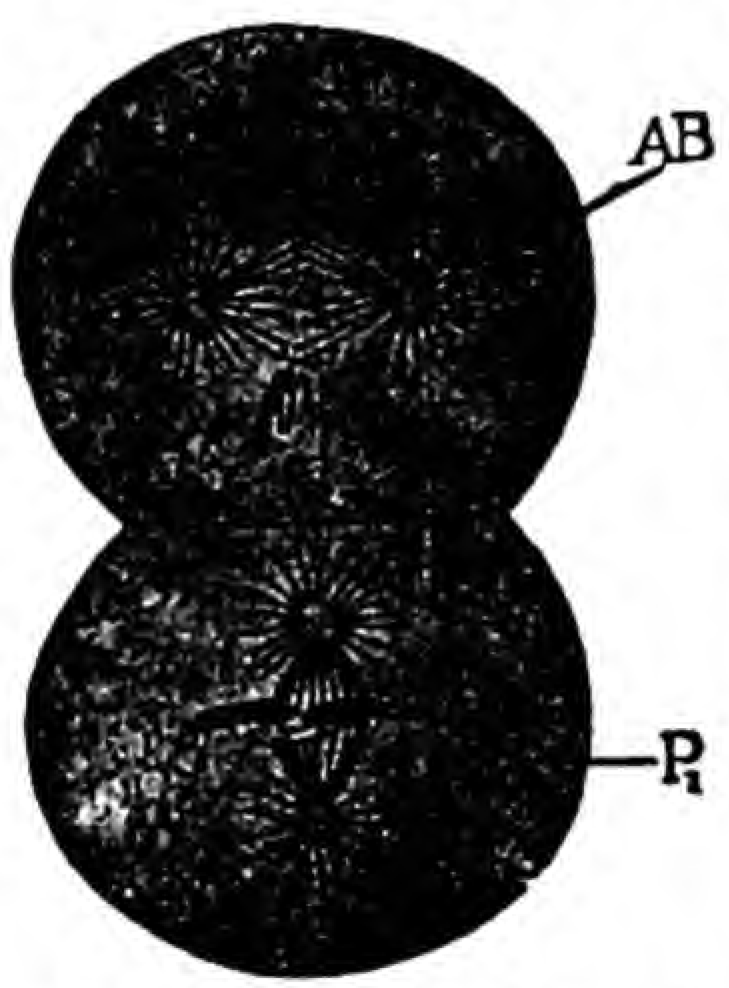


FIG. 249.—The two-cell stage of the egg of **Ascaris megalocephala** (monovalens) when the spindles for the four-cell stage are being formed, showing diminution of the chromatin. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Boveri.)

derm as well as to the ectoderm of the stomodæum (œsophagus). E is the primordial endoderm cell, which gives rise at first to E_1 and E_2 (Fig. 251), from which later the entire endodermal layer of the intestine is derived. P_3 divides into P_4 and D (Fig. 251); finally P_4 divides into the primordial sexual cells G_1 and G_2 (Fig. 252). D gives rise to the so-called tail-cells, which, together with the descendants of C (Fig. 250 D), take part in the formation of the ectoderm and mesoderm. A blastocœle is formed at the sixteen-cell

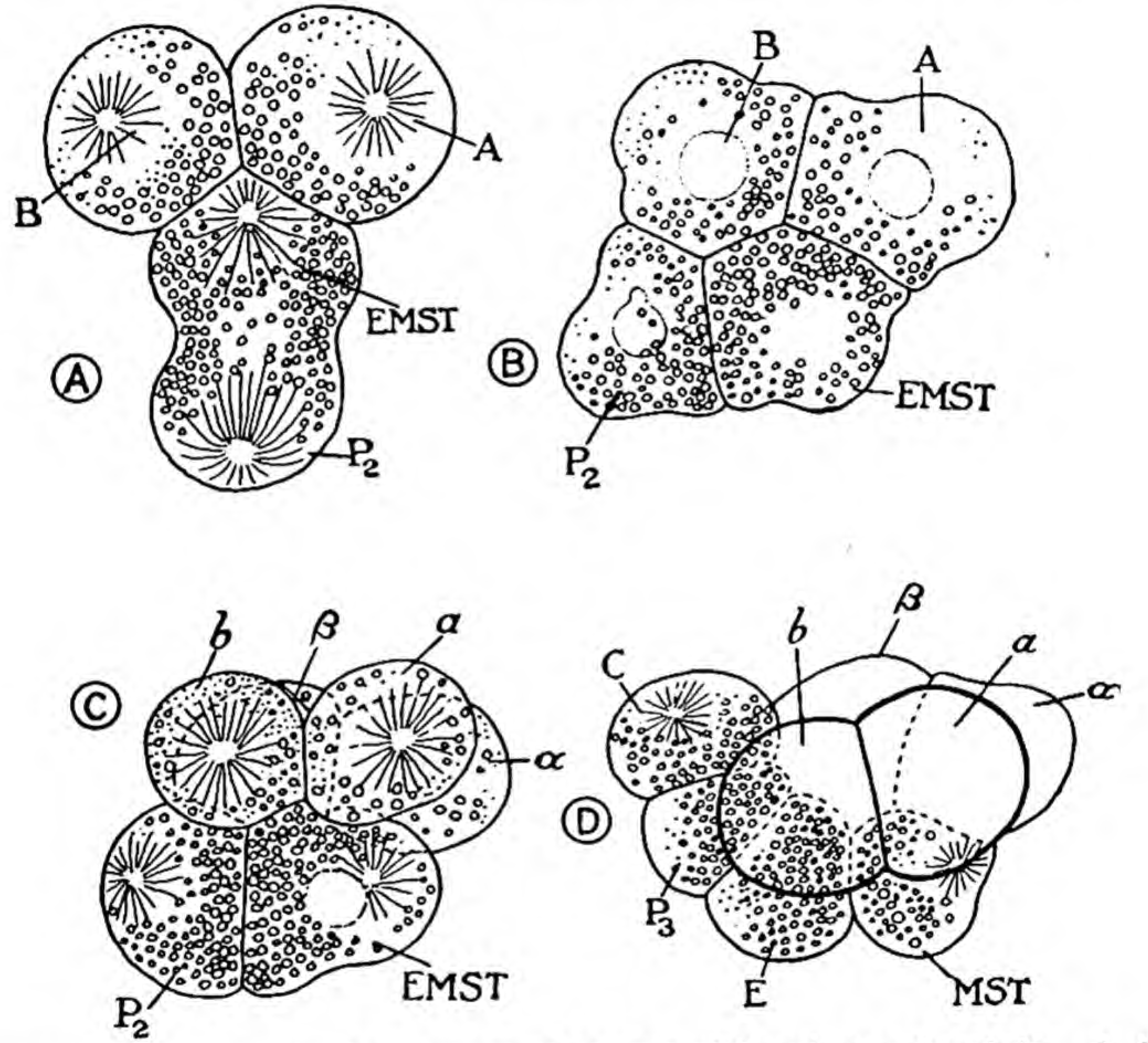


FIG. 250.—Early stages in the cleavage of the egg of **Ascaris megalocephala.** *A*, four-cell stage in the T-condition seen from the right side; *B*, four-cell stage in the rhomb condition seen from the right side; *C*, six-cell stage seen from the right side; *D*, eight-cell stage seen from the right side. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Boveri.)

stage, and the gastrulation is a kind of invagination. The nuclei of all but the primordial genital cells (Fig. 252, G_1 and G_2) loose a large part of their chromatin; the somatic cells are therefore described as degenerate in comparison with the primordial genital cells.

Many of the Nematoda have a curious and complex **life-history**: a few examples will be selected for description.

Angiostomum nigrovenosum lives, in the sexual condition, in the lungs of Frogs and Toads: it is remarkable among members of the class in being

hermaphrodite. The eggs are laid and the embryos pass from the lungs into the enteric canal of the host, are expelled with its fæces, and develop in water into a sexual Nematode, called the *Rhabditis*-form, in which the sexes are separate: in this the fertilized eggs develop in the body of the female, and, when fully formed, make their way through the wall of the uterus and proceed to devour the whole of the maternal tissues, leaving nothing but the cuticle. Being set free, they live in mud until they succeed in gaining access to a frog's mouth, when they pass into the lung, develop hermaphrodite reproductive organs, and so re-commence the cycle. It will be seen that we have here a peculiar form of alternation of generations, distinguished not by the alternation of a sexual with an asexual form (metagenesis) as in Hydrozoa, but by

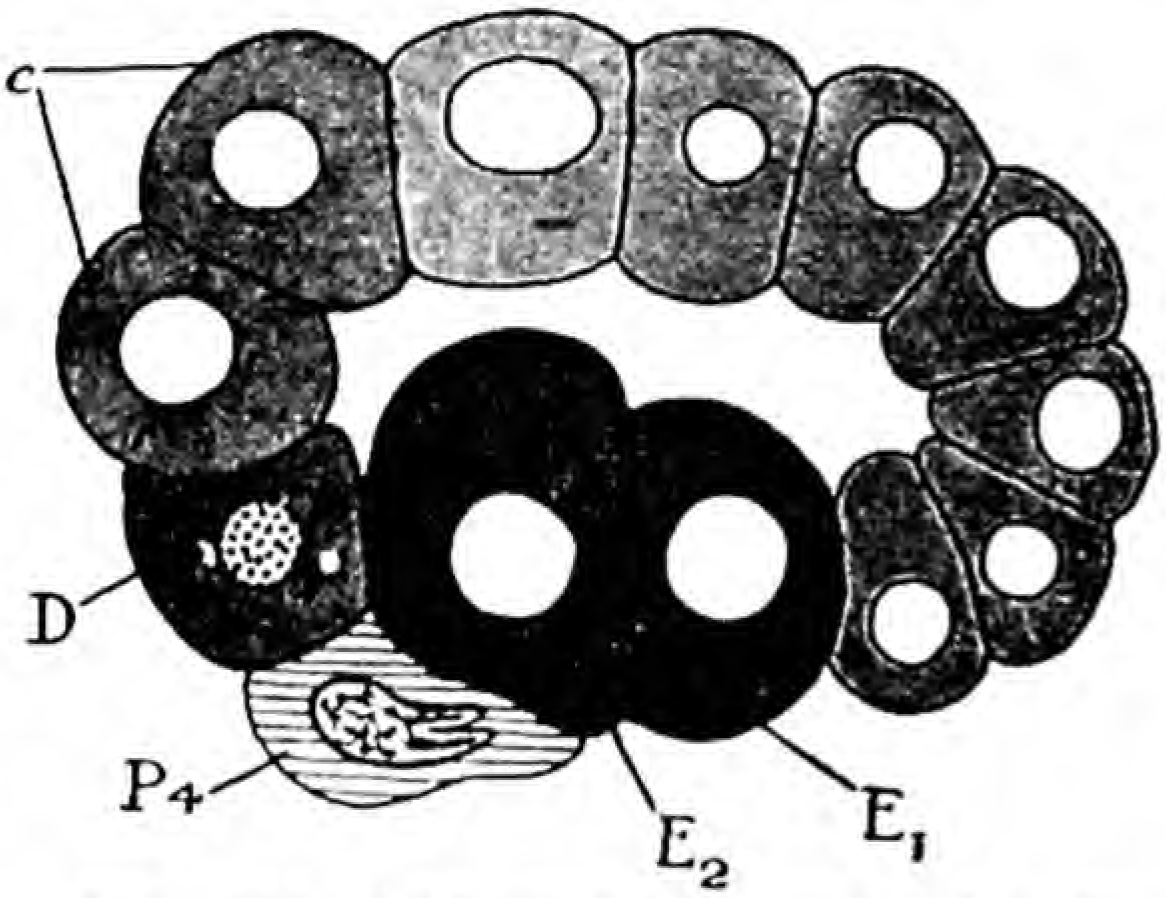


FIG. 251.—Optical median sagittal section through the blastula of **Ascaris megalocephala** at the time when the process of gastrulation is commencing. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Boveri.)

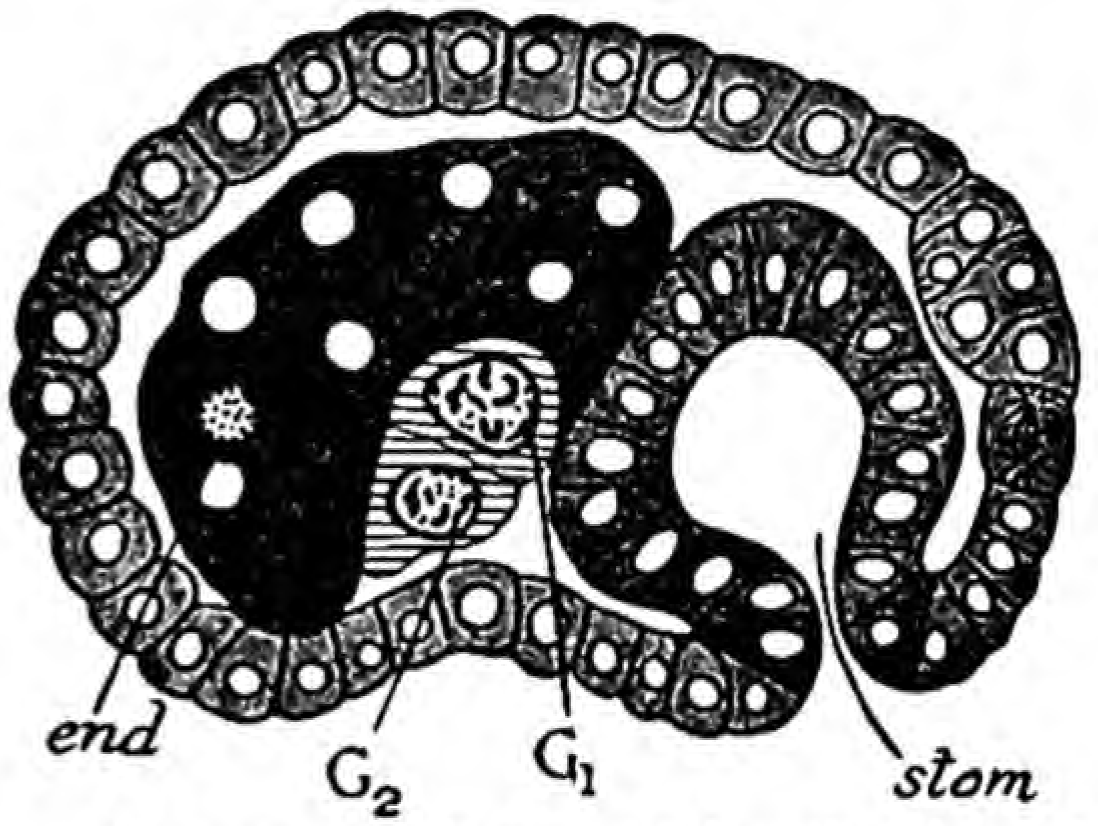


FIG. 252.—Median sagittal section through an embryo of **Ascaris megalocephala** after the invagination of the primordial genital cells and the stomodæum. *end*. endoderm; G^1, G^2, primordial genital cells; *stom*. stomodæum. (From MacBride's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Boveri.)

the alternation of a hermaphrodite with a diœcious form—a variety of *heterogamy*.

One of the most terrible parasites of Man is *Trichinella spiralis* (Fig. 253), a minute worm, the male (*C*) a little over 1 mm. ($\frac{1}{18}$ in.) in length, the female (*B*) about 3 mm. ($\frac{1}{8}$ in.). In the adult or sexual condition it lives in the intestine of Man, the Pig, and other Mammals such as Rats.

The adult females, which are viviparous, leave the cavity of the intestine and bore into its wall, usually reaching the interior of one of the lacteal vessels of the lymphatic system. Here they deposit their young (*B, e*) to the number of as many as a thousand or more at a time. These are carried passively in the stream of lymph, perhaps ultimately in the blood-stream, and are thus distributed throughout the body. Eventually they travel into the system of voluntary muscles, such as those of the limbs, back, tongue, etc. Each worm then penetrates the sarcolemma of a muscle-fibre and coils itself up in the

muscle substance (*A*); a spindle-shaped cyst (*cy.*) is formed round it, and the muscle undergoes more or less degeneration. This process gives rise to various morbid symptoms in the host, but after some months the cysts become calcified, and the danger to the infected individual is over. The flesh of a "trichinized" human subject has been estimated to contain 100,000,000 encysted worms, and that of an infected pig 85,000 to the ounce. In order that further development of the encysted and sexless Trichinæ should take place, it is necessary for the infected flesh of the host to be eaten by another animal in which the worm is capable of living, *e.g.*, that of a Pig by Man. When this is done the cysts are dissolved by the digestive juices, the worms escape, develop reproductive organs, and copulate, the young migrating into the muscles and producing the disease as before. The result of eating an ounce of "trichinized" or "measly" pork, improperly cooked, might be the liberation in the human intestine of perhaps 80,000 worms; and, if half of these were females, each producing 1,000 embryos, some 40,000,000 worms would shortly begin to migrate into the muscles, and produce the various symptoms of "trichinosis."

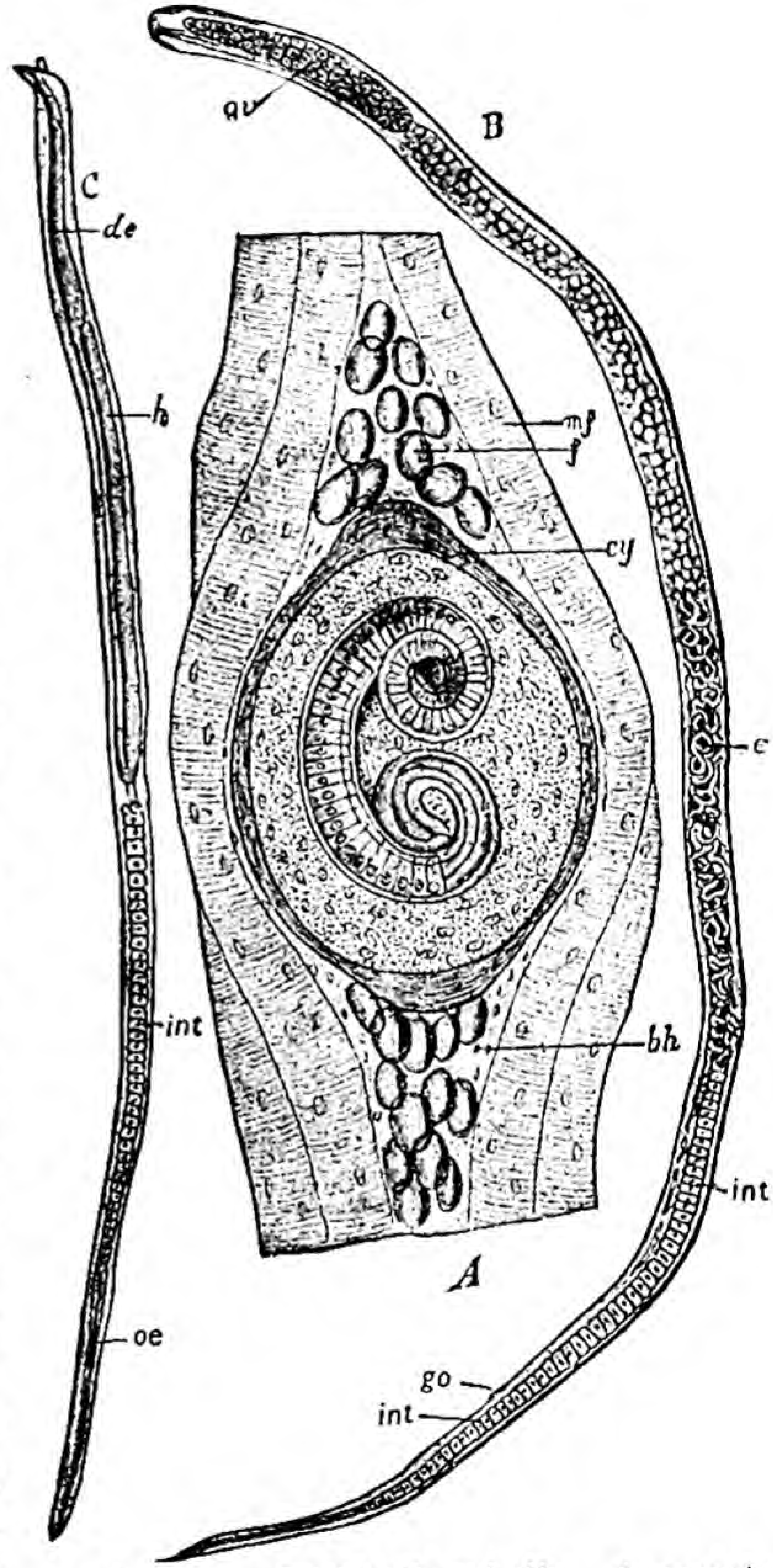


FIG. 253.—**Trichinella spiralis.** *A*, encysted form, in muscle of host; *B*, female; *C*, male. *bh.* connective-tissue envelope; *cy.* cyst; *de.* ejaculatory duct; *e.* embryos; *f.* fat-globules; *go.* gonopore; *h.* testis; *int.* intestine; *m. f.* muscle-fibre; *oe.* pharynx; *ov.* ovary. (From Lang's *Comparative Anatomy*, after Claus.)

It will be noted that in this case the parasite is able to exist in various hosts, and that both sexual and asexual stages are passed through in the same host, dispersal of the species taking place by the flesh of an infected animal being eaten by another, either of the same or of a different species.

The female Guinea-worm (*Filaria medinensis*) attains a length of 30–200 cm. (1–6 ft.), and lives in the subcutaneous connective-tissue of the legs of

Man. The eggs develop in the uterus, and the new-born young pass out of the body of the host through abscesses caused by the presence of the parasite. If, as must often be the case, they escape into water, they make their way into the body of a Water-flea (*Cyclops*), which is the intermediate host, and in this condition probably reach their human host once more in his unfiltered drinking-water. *Filaria bancrofti* and other species are, in the larval condition, parasites in the blood of man. The adult females of *F. bancrofti* live normally in the lymphatic vessels. They are viviparous, and the young when they escape reach the blood and are thus distributed. Normally they are to be found in the peripheral vessels only at night-time, when the superficial vessels are more dilated and thus permit of their passage. They are transmitted from one human host to another by the agency of mosquitoes, which act as intermediate hosts. *F. bancrofti* is very widely distributed in tropical countries, and is the cause of a disease called *filariasis*, with a variety of symptoms—such as anæmia, lymphatic tumours, elephantiasis.

Finally the life-history of one of the plant parasites among the Nematoda—viz., *Tylenchus scandens* (*Anguillula tritici*)—may be mentioned. The immature animal infects the stem of young wheat plants and then enters the flower of the plant, where it matures. The sexes are separate, and mating takes place in the wheat flower. The embryos hatching from the eggs remain in the grain, which is pathologically changed into a brown gall. The larvæ spend the winter either in the infested grain or free in the soil. They show a great capacity for survival in a dormant and desiccated condition. In spring new infection of wheat plants takes place.

APPENDIX TO THE NEMATODA.

Family *Chætosomatidæ*.

This family includes several genera of small marine worms, *Chætosoma* (Fig. 254), *Tristicochæta*, *Rhabdogaster*, and others, which are sometimes included among the Nematoda.

The body is elongated, its anterior region being sometimes dilated to form a head. Either the whole body or the dorsal surface only is beset with fine setæ, and there may be a double row of movable chitinoid hooks round the head. The ventral surface bears posteriorly curious *locomotor rods* (*f.*), either hooked or with knobbed ends: by these the animals crawl. The mouth is anterior and terminal, the anus posterior and ventral, and there is a muscular pharynx. The sexes are separate. The male has a single testis: the vas deferens opens along with the anus: there are two penial setæ. The female has paired ovaries and a single vagina opening near the middle of the body on the ventral side.

Family *Desmoscolecidæ*.

Desmoscolex is also a minute marine worm, having a globular head and a variable number of segments (Fig. 255). The head bears four movable chitinoid rods or setæ, and a pair of similar structures occurs on many of the other segments. The terminal mouth leads by a muscular pharynx into a straight intestine: the anus is dorsal in position. The animal is diœcious; the gonads have the form of simple sacs, the testis opening along with the

anus, the ovary on the ventral surface anterior to the anus. The male has a pair of penial setæ.

Trichoderma has some superficial resemblance to Desmoscolex, but is nearer the ordinary Nematodes.

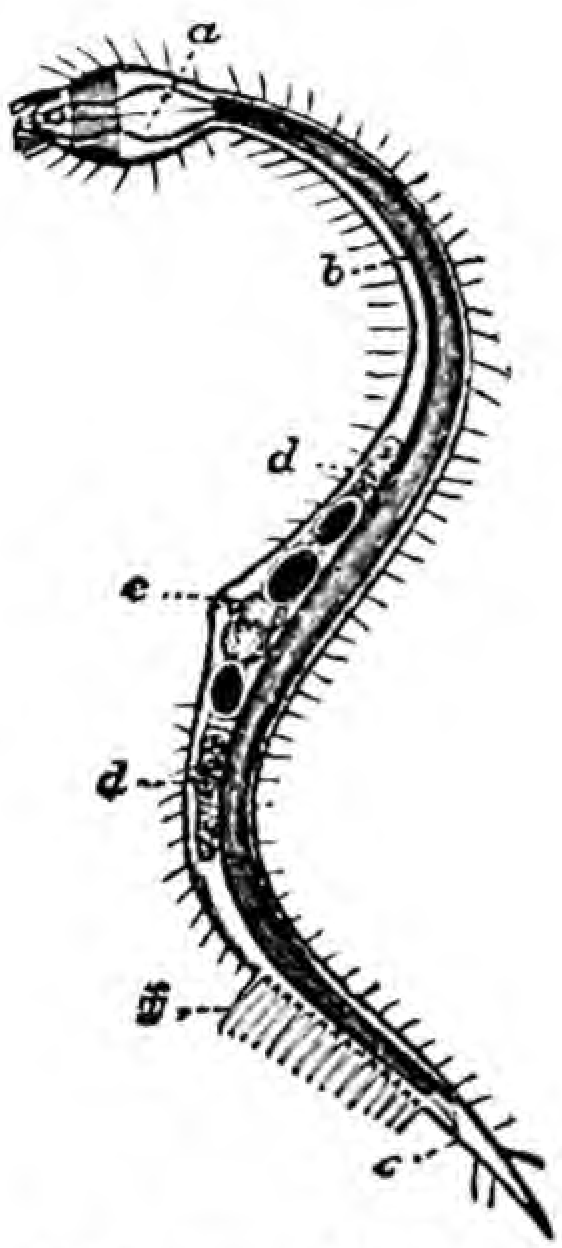


FIG. 254.—Mature female of **Chætosoma claparedii.** × 57. *a.* œsophagus; *b.* intestine; *c.* anus; *d. d.* ovaries; *e.* generative pore; *f.* locomotor rods. (From Shipley, after Metschnikoff.)

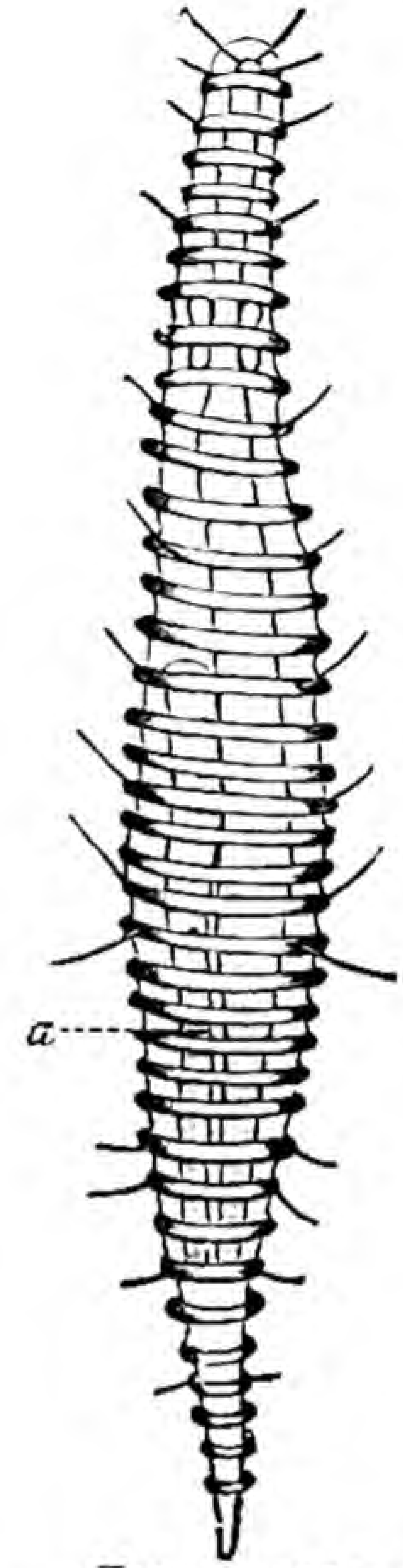


FIG. 255.—Female **Desmoscolex,** ventral view, × 260. *a.* ovary. (From Shipley, after Panceri.)

THE NEMATOMORPHA.

The Nematomorpha include a small number of greatly elongated, thread-like worms which are parasitic in the asexual, free-living in the sexual stage. There are two families: the *Gordiidæ* and the *Nectonematidæ*.

Gordius aquaticus is found in earth or fresh water, and resembles a tangle of brown string, the length being frequently as much as 15 or 16 cm., while the diameter does not exceed 0·5 mm.

The outer surface of the body is furnished by a cuticle, which is secreted by an epithelial sub-cuticle consisting of a single layer of cells. A ventral median line interrupts the muscles of the body-wall. The muscles are composed of epithelio-muscular cells.

In the larva the body-cavity is filled with polygonal parenchyma cells. Later, fissures appear in these cells and increasing in extent, eventually give rise to extensive canal-like cavities—a median ventral and two lateral, with, in the female, a narrow median dorsal, separated from one another for the most part by comparatively thin partitions of parenchyma sometimes termed

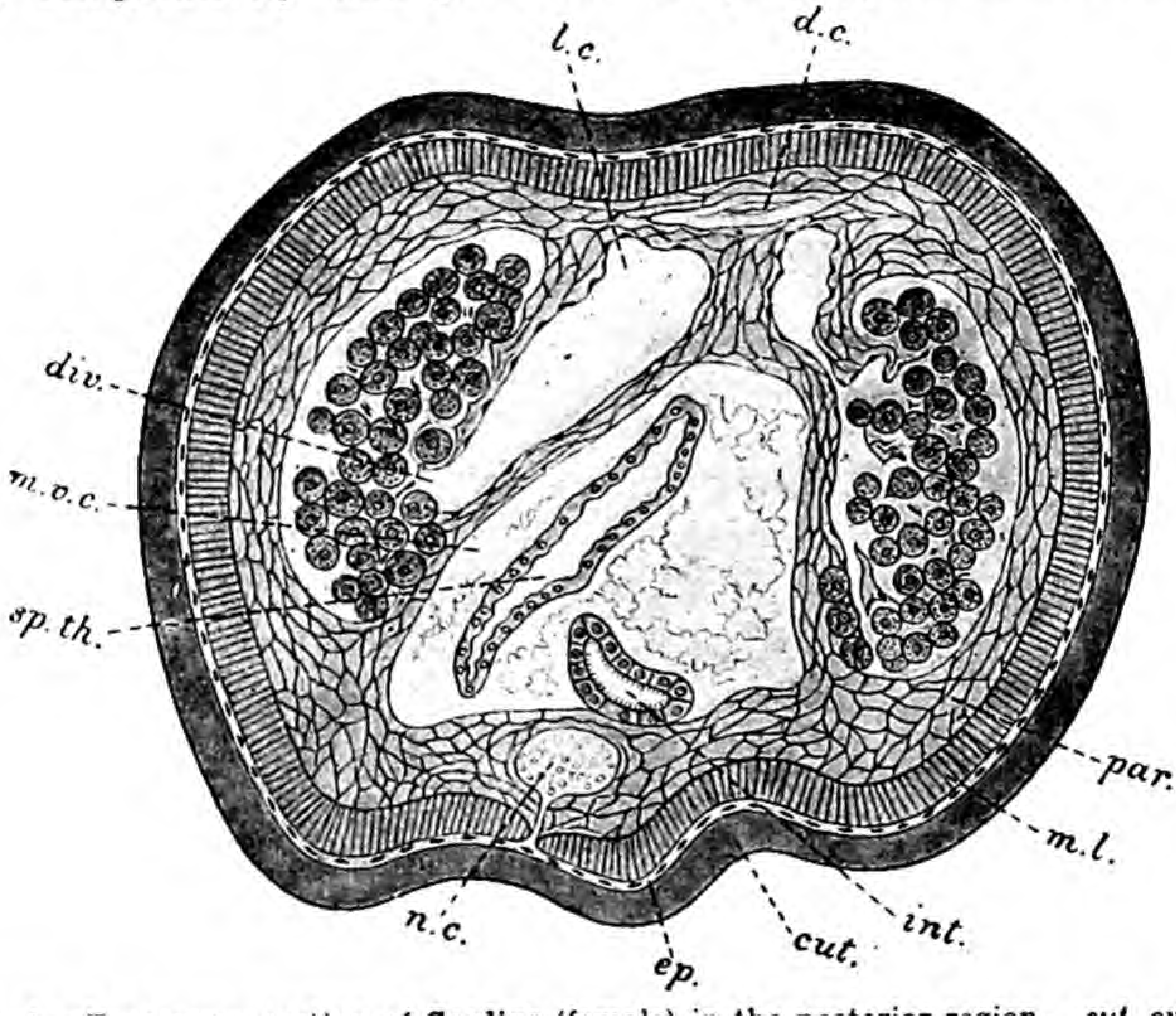


FIG. 256.—Transverse section of **Gordius** (female) in the posterior region. *cut.* cuticle; *d. c.* dorsal canal; *div.* diverticulum of lateral canal; *ep.* deric epithelium; *int.* intestine; *l. c.* lateral canal; *m. l.* muscle layer; *m. v. c.* median ventral canal; *n.c.* nerve-cord; *par.* parenchyma; *sp.th.* spermatheca. (After Rauther.)

mesenteries. The median ventral canal (Fig. 256, *m. v. c.*) of the body-cavity encloses the alimentary canal: the lateral canals (*l. c.*) are associated with the development of the reproductive apparatus. In the case of the lateral alone, and only in the female, is there an epithelial lining.

Excretory organs appear to be missing.

The nervous system consists of a pharyngeal ring of great thickness (brain), which is continued into a single ventral cord composed of three strands containing nerve-cells. Eye spots have been described in the free-living sexual state.

The sexes are distinct. In the female Gordius (Fig. 257, *C*) the lateral canals of the body-cavity (*ut.*) are modified to act as ovaries and oviducts.

They give off a series of regularly arranged lateral diverticula from the cells lining which the ova are derived (Fig. 257, *A*, and Fig. 256, *div.*). Posteriorly, each of these lateral canals becomes a narrow tube or oviduct. These open into a median chamber with glandular walls, the uterus (*vag.*), and into this there also opens the duct of a *spermatheca* or *receptaculum seminis* (*spth.*) for the reception and storage of the sperms received in copulation. The uterus is continued backwards by an atrial cavity opening along with the intestine in a cloacal aperture (Fig. 257, *gnp.*) at the posterior end of the body. In the male (Fig. 257, *B*) the lateral canals are unsegmented tubes—testes or spermsacs (*vs. sem.*)—from the cells bordering a portion of which sperms are developed. From each of these at its posterior end a narrow vas deferens passes backwards to open into the cloaca (*cl.*). The latter, with a ventrally-placed opening, has

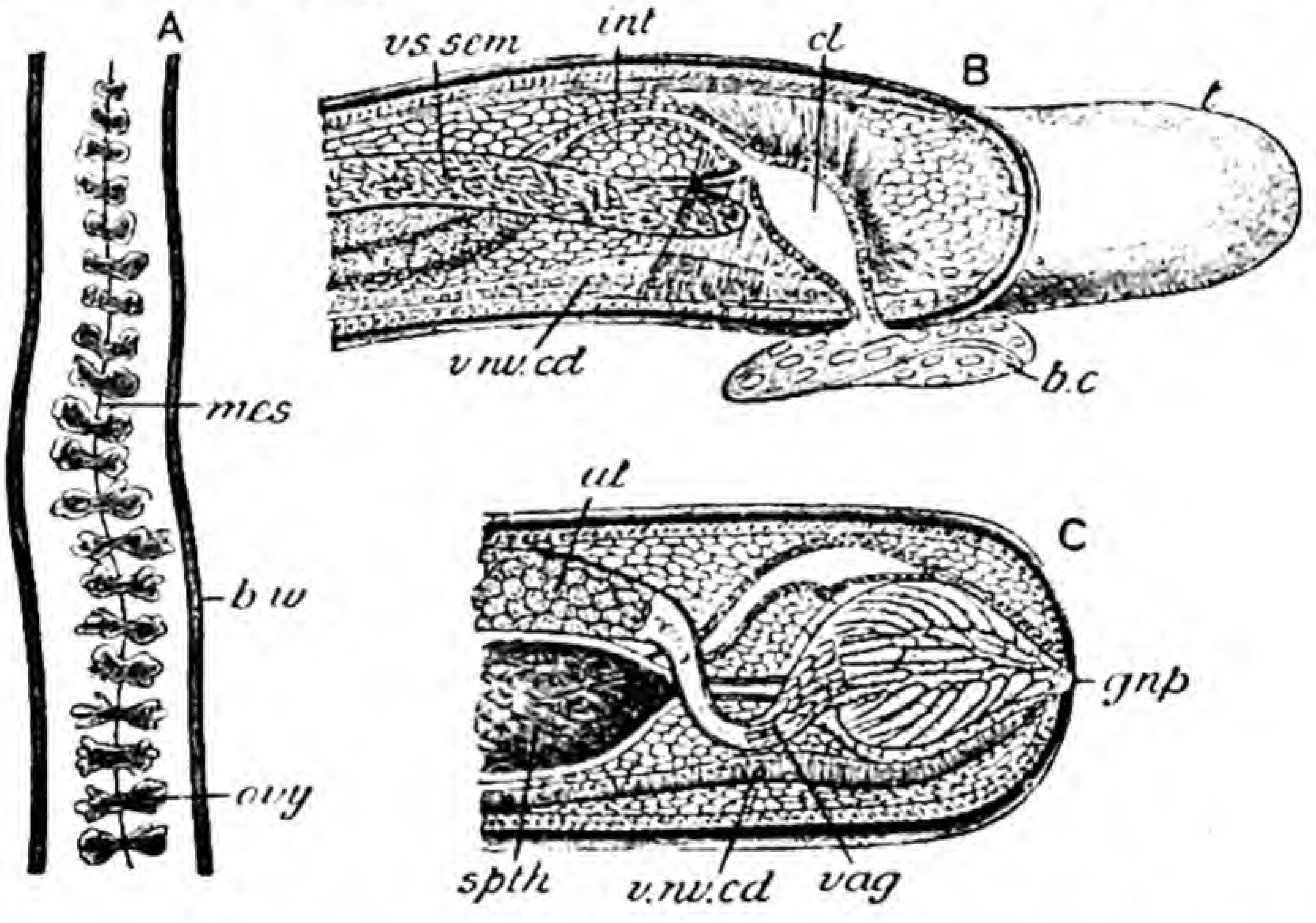


FIG. 257.—**Gordius.** *A*, horizontal section of female, showing ovaries (*ovy.*) attached to mesentery (*mes.*); *b.w.* body-wall. *B*, posterior extremity of male, sagittal section. *b. c.* coagulated mass of sperms (?); *cl.* cloaca; *int.* intestine; *t.* tail; *v. nv.cd.* ventral nerve-cord; *vs. sem.* vesicula seminalis or sperm-sac. *C*, posterior extremity of female, sagittal section. *gnp.* cloacal aperture; *spth.* spermatheca; *ut.* lateral canal; *vag.* uterus, followed posteriorly by atrium; *v. nv.cd.* ventral nerve-cord. (After Vejdowsky.)

a muscular wall and is probably capable of being everted to serve as a penis. In the sexual state the enteric canal undergoes more or less complete degeneration.

Nectonema differs from Gordius by having two rows of fine bristles running along either side of the body. The body-musculature is divided by both a dorsal and a ventral line; the body-cavity in the female is reduced to a narrow space between the wall of the ovary and the muscular layer; in the male it is considerably wider. The genital apparatus is simpler than in Gordius, and the ovary is not segmented.

When immature the Nematomorpha live in the body-cavity of Arthropods; on gaining maturity they become free-living. Gordius lives in fresh water; Nectonema is marine.

THE ACANTHOCEPHALA.

This class contains a number of genera of parasitic worms, of which *Echinorhynchus* is the chief. The present section will be devoted to this genus, a not uncommon parasite in the intestine of Mammals, Birds, Reptiles, Amphibians, and Fishes. The largest species, *E.* (*Gigantorhynchus*) *gigas*, is found in the Pig (Fig. 258, *A*), and has once been recorded in the human

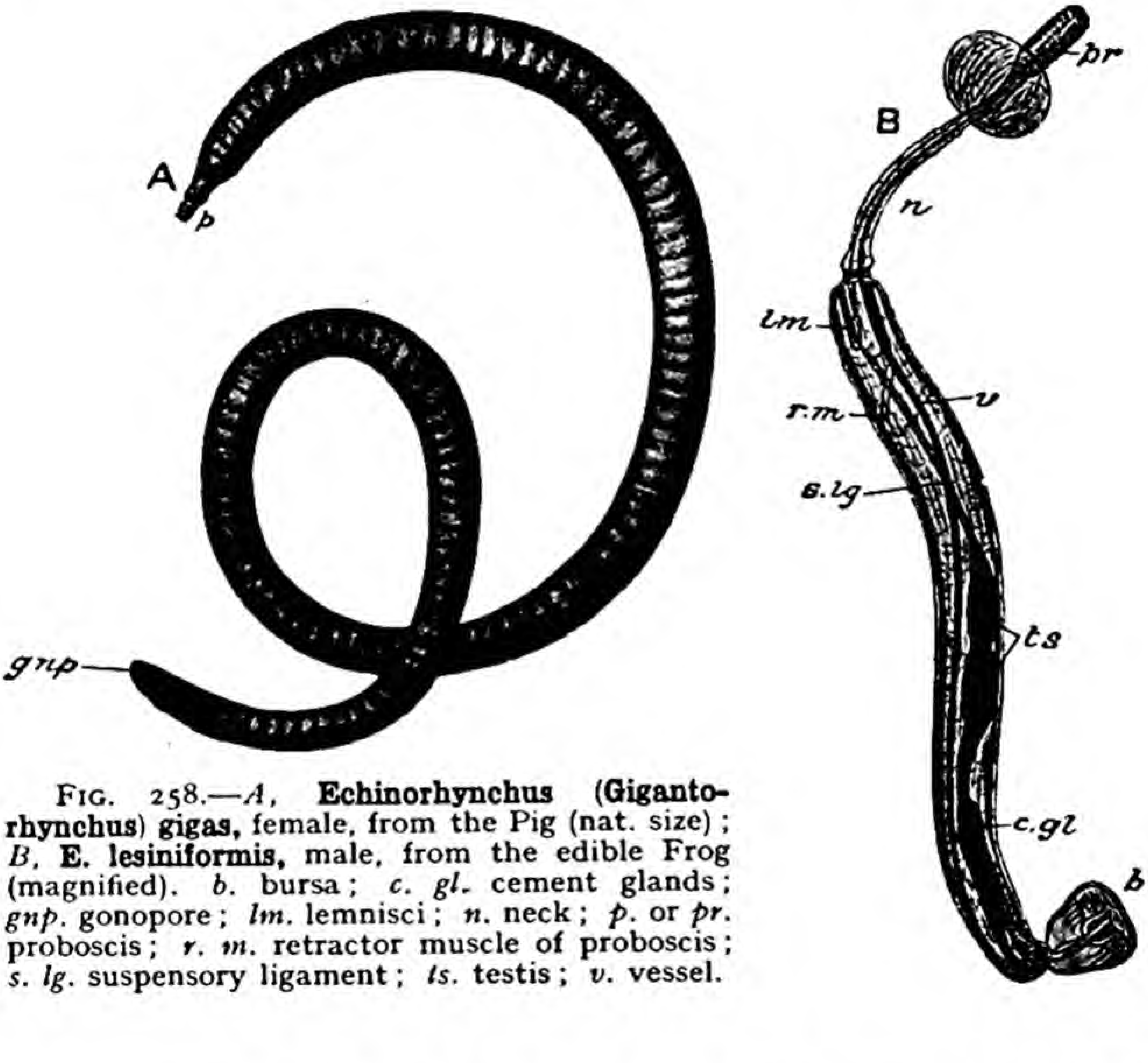


FIG. 258.—*A*, **Echinorhynchus (Gigantorhynchus) gigas,** female, from the Pig (nat. size); *B*, **E. lesiniformis,** male, from the edible Frog (magnified). *b.* bursa; *c. gl.* cement glands; *gnp.* gonopore; *lm.* lemnisci; *n.* neck; *p.* or *pr.* proboscis; *r. m.* retractor muscle of proboscis; *s. lg.* suspensory ligament; *ts.* testis; *v.* vessel.

subject: it may attain, in the female, a length of 50 cm., or more than half a yard. Most species are small, not exceeding 1 cm. in length.

External Characters.—The body is cylindrical, and ends in front in a protrusible portion, the *proboscis* (*A*, *p.*, *B*, *pr.*), which is cylindrical and is covered with many rows of recurved chitinoid hooks. The worm lies with the proboscis sunk in the wall of the intestine of its host, which is sometimes riddled with holes formed in this way. In some species there is a distinct neck (*B*, *n.*) between the proboscis and the trunk, and there may be a globular dilatation at the anterior end of the neck. At the hinder end of the body is a single aperture, the gonopore or reproductive aperture (*gnp.*): connected with this,

in the male, is a protrusible, bell-like structure, the *bursa* (*b.*), which acts as a copulatory organ, like the somewhat similar organ in certain Nematoda. There is no trace of mouth, anus, or excretory pore.

The **body-wall** is covered with a stout cuticle, beneath which is a striated protoplasmic layer, probably representing the ectoderm. Then comes a layer of transverse, and then one of longitudinal muscles. The body-wall thus constituted encloses a spacious **body-cavity** containing a clear fluid.

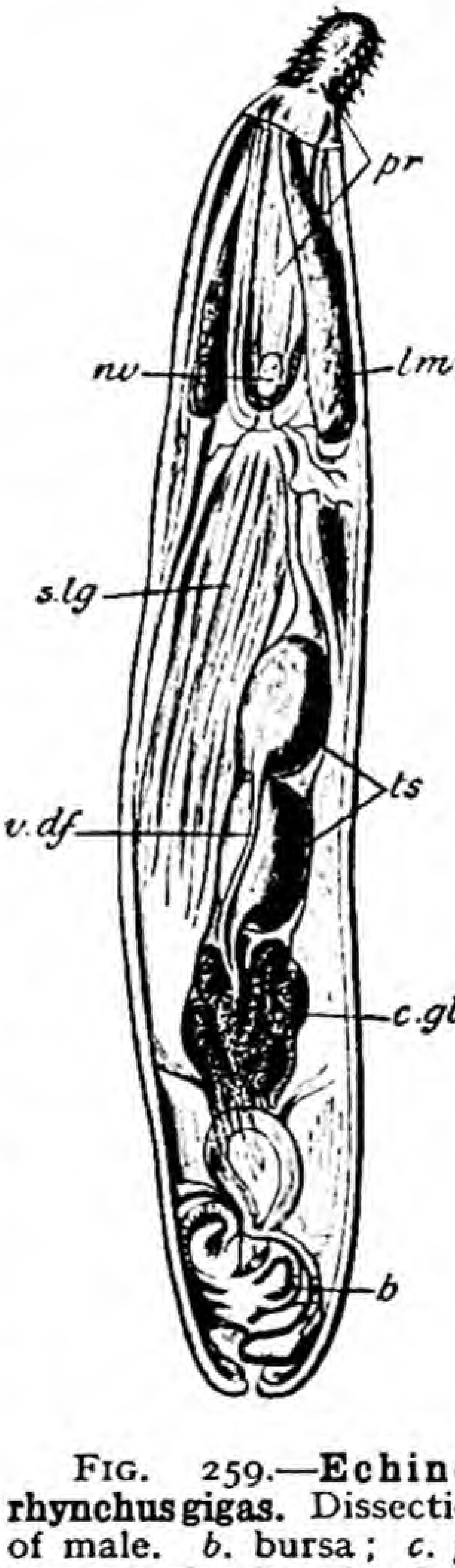


FIG. 259.—**Echinorhynchus gigas.** Dissection of male. *b.* bursa; *c. gl.* cement glands; *lm.* lemnisci; *nv.* nerve-ganglion; *pr.* proboscis; *s. lg.* suspensory ligament; *ts.* testis; *v. df.* vas deferens. (After Leuckart.)

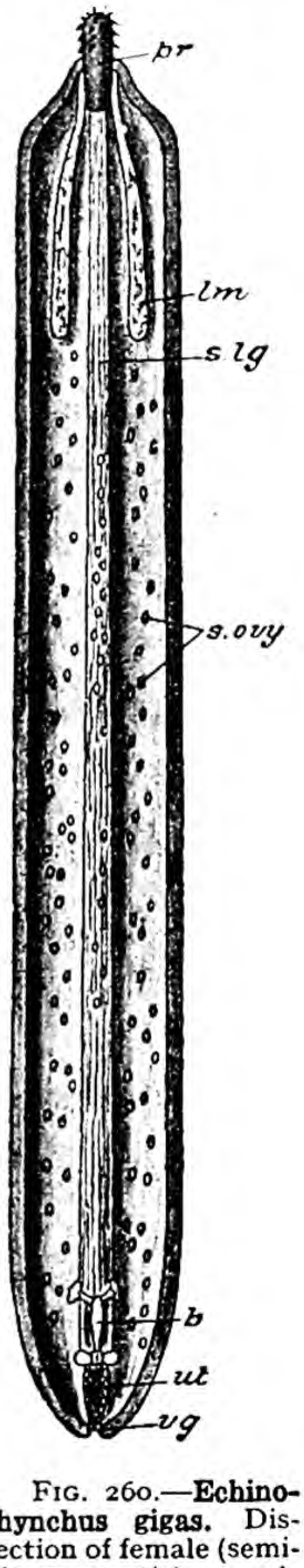


FIG. 260.—**Echinorhynchus gigas.** Dissection of female (semi-diagrammatic). *b.* bell; *lm.* lemnisci; *pr.* proboscis; *s. ovy.* swimming ovaries; *ut.* uterus; *vg.* vagina.

In correspondence with the absence of mouth and anus there is no trace of enteric canal, the Acanthocephala resembling in this respect the Cestoda, the only other class of Metazoa which is entirely anenterous. Food is thus, as in Tapeworms, taken entirely by absorption by the general surface of the body.

The proximal end of the *proboscis* is contained in a muscular sheath sunk in the anterior end of the trunk, and is provided with four retractor muscles (Fig. 258, *r. m.*). The muscles of the sheath are circular and act as protractors. At the sides of the base of the proboscis two club-shaped organs, the *lemnisci* (*lm.*), hang down into the body-cavity. Their function is quite unknown.

In the body-wall run two longitudinal **vessels** (*v.*) containing a granular fluid, and connected with a network of fine canals in the proboscis, bursa, etc. The function of these vessels is not known with certainty: they may have to do with the absorption and circulation of nourishment.

The **central nervous system** (Fig. 259, *nv.*) is represented by a single large

ganglion placed at the base of the proboscis, and sending off nerves in various directions. In the male there are also two ganglia supplying the reproductive organs. Sense-organs are wholly absent.

A pair of remarkable **excretory organs** (Fig. 261) have been found to occur in Echinorhynchus gigas. These consist of a pair of ramified protoplasmic masses situated in the body-cavity at the posterior end, near the genital aperture. In the interior is a system of branching canals, the terminal branches of which, each contained in one of the terminal lobes of the tree-like organ, are provided with ciliary flames; at the end of each lobe are a number of fine perforations placing the contained canal in communication with the body-cavity. The stalk of each excretory organ contains a single main canal; these unite to form a wide median dorsal channel which opens behind in the female into the unpaired portion of the oviduct and in the male into the ejaculatory duct.

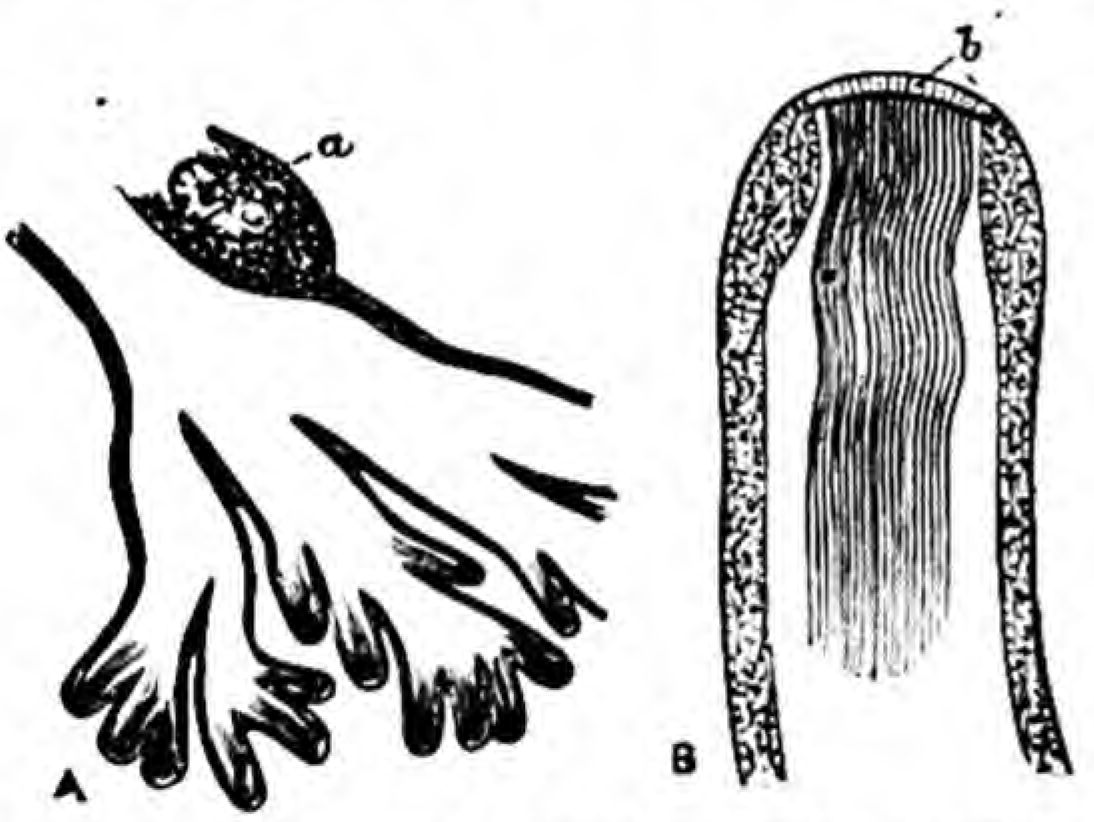


FIG. 261.—*A*, longitudinal section through the terminal twigs of the excretory organ of **Echinorhynchus gigas**; highly magnified. *a*, nucleus. *B*, a terminal twig more highly magnified. *b*, the porous membrane. (From Shipley, after Kaiser.)

The greater part of the body-cavity is occupied by the **reproductive organs.** The sexes are separate, and the female is larger than the male. In both sexes the gonads and their ducts are connected with a great *suspensory ligament* (*s. lg.*), which extends backwards from the end of the proboscis-sheath.

In the male there are two ovoidal *testes* (Fig. 259, *ts.*) connected with the suspensory ligament. From each a *vas deferens* (*v. df.*), furnished with several *vesiculæ seminales* or sacs for the storage of spermatic fluid, passes backwards and unites with its fellow to form an *ejaculatory duct*, with which are connected about half a dozen *cement glands* (*c. gl.*). The ejaculatory duct opens into the bursa or bell-like copulatory organ (*b*), and has at its opening a small papilla acting as a penis.

In the female the ovary is connected with the suspensory ligament (Figs. 260 and 262, *s. lg.*). When ripe, groups of ova—known as the "swimming ovaries" (*s. ovy.*)—become detached and swim freely in the body-cavity, where they are fertilized. The ducts are very peculiar. Connected with the end of the suspensory ligament is a muscular *uterine bell* (*b.*), widely open anteriorly (Fig. 262, *x.*) into the body-cavity, and having towards its posterior end a small aperture or a pair of small apertures (*y*), also communicating with the body-cavity. The bell is connected with a narrow double passage leading to a uterus (*ut.*), which itself opens by the genital aperture at the posterior end of the body. The uterine bell performs rhythmical swallowing movements, and as the eggs—containing partly developed embryos—float in the body-cavity they

are swallowed by the bell. The immature eggs, which are globular, are passed back into the body-cavity through the posterior aperture (y) of the bell; but the mature eggs, which are spindle-shaped and covered with a chitinous investment, make their way from the bell to the uterus through the narrow passages, and so to the vagina.

The early stages of **development** take place in the body-cavity. Cleavage is regular, and a peculiar form of gastrula is produced, having neither archenteron nor blastocœle—in other words the ectoderm and endoderm are in close contact with one another, and no central cavity is enclosed by the latter. The ectoderm layer, which is devoid of cell-limits, secretes a cuticular membrane investing the embryo; then a second membrane is formed within the first, and a third within the second; the embryo thus comes to be enclosed in a triple case (Fig. 263), which differs from an egg-shell in being formed by the developing ectoderm. At what will become the anterior end chitinoid hooks appear.

At about this period the embryo is born, and reaching the intestine of the host, is extruded with its fæces. Its further development depends upon its being swallowed by an intermediate host, which, in the case of *E. gigas* of the Pig is a maggot, the larva of a Beetle, *Cetonia aurata*. The Echinorhynchi of fresh-water Fish have for their intermediate host certain small fresh-water Crustacea belonging to the genera *Gammarus* and *Asellus*.

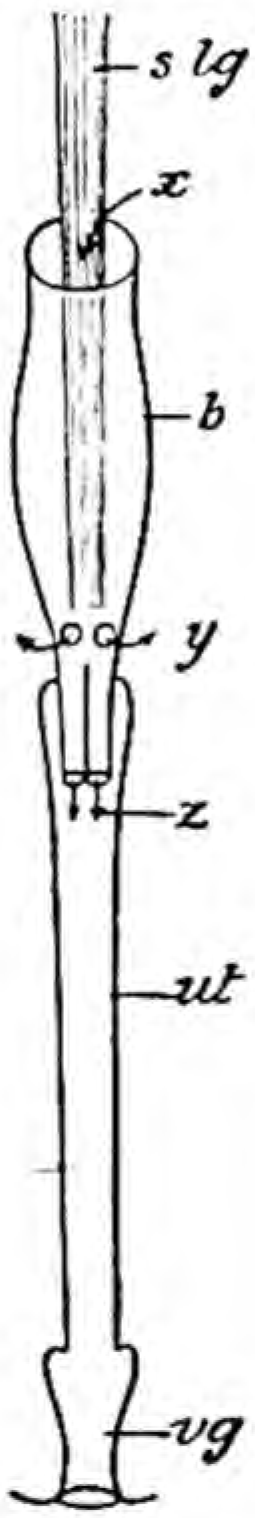


FIG. 262.—Female organs of **Echinorhynchus.** *b.* uterine bell; *s. lg.* suspensory ligament; *ut.* uterus; *vg.* vagina; *x*, *y*, apertures of bell; *z*, apertures leading from bell to uterus. (After Hertwig.)

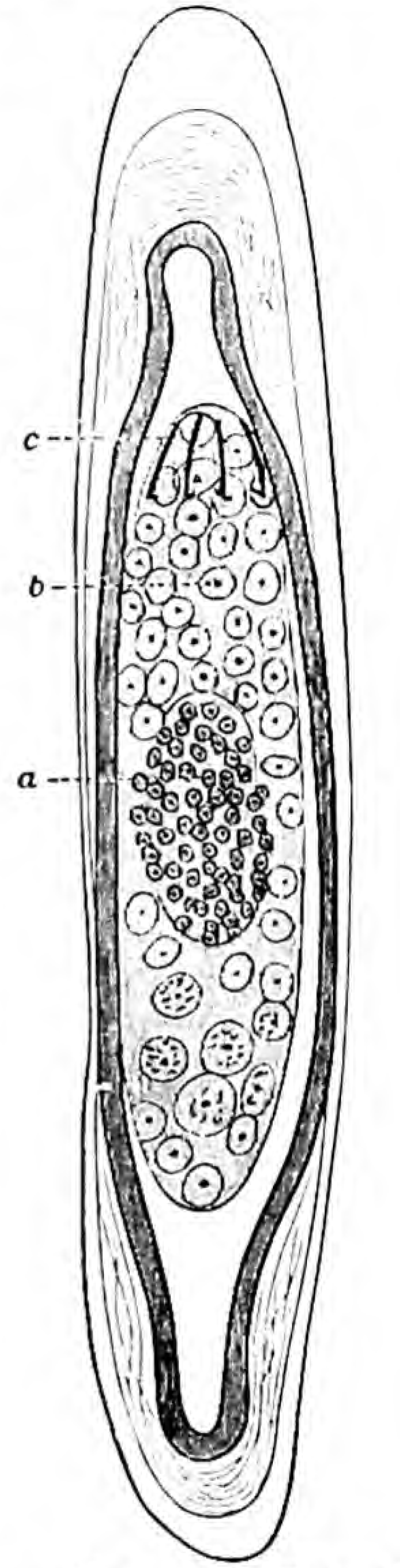


FIG. 263.—Egg of **Echinorhynchus acus,** enclosed in a triple case; highly magnified. *a.* endoderm; *b.* ectoderm; *c.* chitinous hooks. (From Shipley, after Hamann.)

Having reached the intestine of the intermediate host, the chitinoid embryonic membranes are dissolved by its digestive juices, and the embryo either fixes itself to the wall of the intestine or makes its way into the body-cavity; in either case it soon begins to undergo further development. The endoderm hitherto a solid mass of cells, undergoes a process of splitting, becoming divided into an outer layer in contact with the ectoderm and a solid central axis.

The latter gives rise to the reproductive organs and the suspensory ligament, the outer layer to an epithelium, from which the body-muscles arise; the cavity formed by the splitting of the endoderm is the body-cavity. Part of the proboscis and its sheath are also of endodermal origin. The ectoderm gives rise to the protoplasmic layer of the body-wall, to the whole system of vessels, and to the lemnisci. The larval cuticle is thrown off and a new one formed. The larva reaches adult proportions and attains sexual maturity only if the intermediate host is eaten by the permanent host.

THE ROTIFERA.

The Rotifers, or "*Wheel-animalcules,*" are microscopic creatures, very abundant in pools, gutters, etc., where they occur along with the protozoan fauna

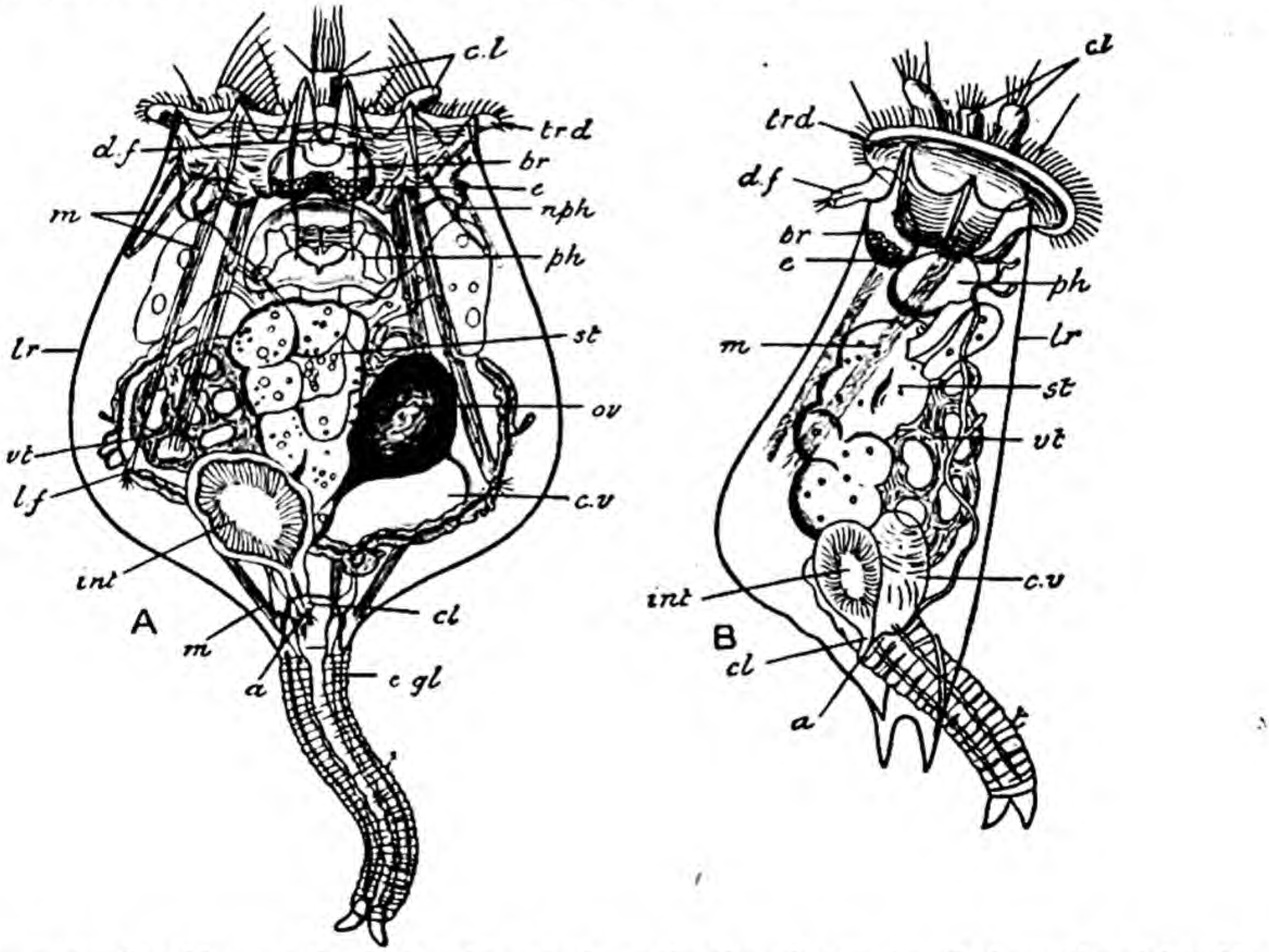


FIG. 264.—**Brachionus rubens**, female. *A*, from the dorsal aspect; *B*, from the right side. *a.* anus; *br.* brain; *d. f.* dorsal feeler; *c.gl.* cement-gland; *cl.* cloaca; *c. l.* ciliary lobes; *c. v.* contractile vesicle; *e.* eye-spot; *int.* intestine; *lr.* lorica; *l. f.* lateral feeler; *m.* muscular bands; *nph.* nephridial tubes; *ov.* germarium; *ph.* pharynx; *st.* stomach; *t.* tail; *tr. d.* trochial disc; *vt.* vitellarium. (After Hudson and Gosse.)

characteristic of these habitats. They had been originally classed with the Ciliophora, to which they bear a superficial resemblance. In spite of their

minute size, they are, however, *true Metazoa*, having an enteric canal, nephridial tubes, gonads, a nervous system and sense-organs.

1. Example of the Class—*Brachionus rubens.*

External Characters.—Brachionus (Fig. 264) is one of the commonest members of the class, being frequently found in abundance in ponds, ditches, etc. The female is about $\frac{1}{3}$ mm. ($\frac{1}{75}$ in.) in length, and is divisible into two distinct parts—a broad anterior region, the *trunk*, and a slender movable *tail* (*t.*). The trunk is enclosed in a glassy cuirass or *lorica* (*lr.*), formed by a thickening of the cuticle and produced into several spines: the tail is wrinkled superficially and ends in two slender processes, together forming a kind of forceps. One surface of the trunk is flattened and, owing to the position of the mouth, is considered as *ventral*; the opposite or *dorsal* surface is convex both from before backwards, and from side to side.

The anterior portion of the body projects from the lorica in the form of a transverse disc (*tr. d.*) with a prominent edge fringed with cilia: this is the *trochal disc*, and is one of the most characteristic organs of the class. By the action of the cilia the animal is propelled through the water, and, as in Vorticella, their successive flexion gives an appearance of rotation to the disc or "wheel-organ" whence the name of the class is derived. Within the circlet of cilia arise three prominences (*c. l.*) covered with cilia of large size. The trochal disc is not perfectly symmetrical, but has at one part of its circumference a depression in which the mouth lies: this marks the ventral surface. The anus (*a.*) is dorsal in position, and is placed at the junction of the tail with the trunk.

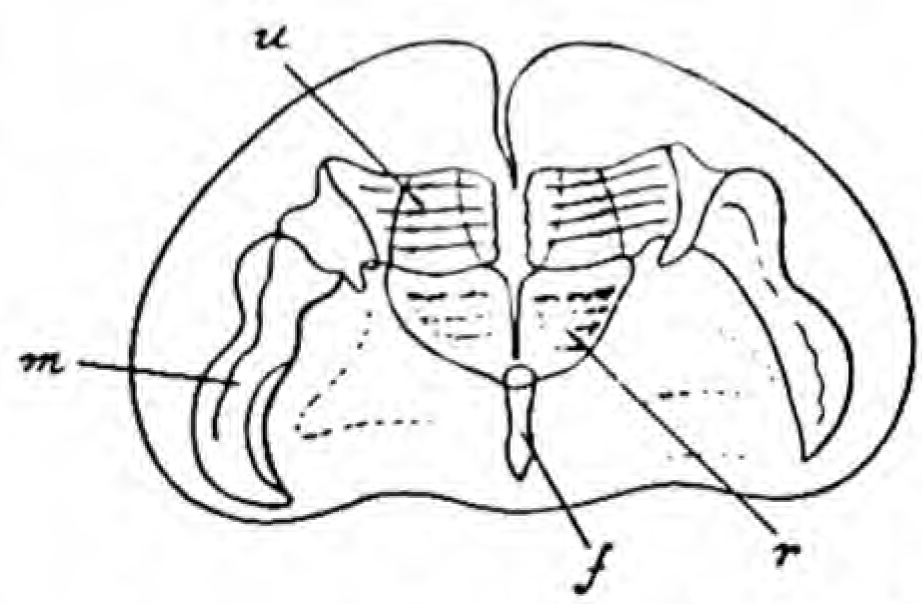


FIG. 265.—Pharynx of **Brachionus rubens.** *f.* fulcrum; *m.* manubrium; *u.* uncus; *r.* ramus. (After Hudson and Gosse.)

The **body-wall** consists of an epidermal layer, without cell-limits, covered by a chitinoid cuticle: it is by a thickening of the latter in the region of the trunk that the lorica is produced. There is no continuous muscular layer, but several bands of unstriped muscle (*m.*) pass from the lorica to the trochal disc in front and to the tail behind, and act as retractors of those organs.

Digestive Organs.—The *mouth* (Fig. 267, *mth.*) lies, as already mentioned, in the ventral region of the trochal disc, anterior to the ciliary circlet but posterior to the three ciliated lobes; it leads by a short *buccal cavity* into a *pharynx* (*ph.*) of peculiar structure known as the *mastax*, and constituting one of the most characteristic organs of the class. The mastax is a muscular chamber (Fig. 265) of rounded form, and contains, as a thickening of its cuticular lining, an elaborate apparatus for triturating the food. In the middle

line is a forked structure, the *incus*, consisting of a small base or *fulcrum* (*f.*) and of two branches or *rami* (*r.*). On either side of the incus is a hammer-like structure, the *malleus*, consisting of a handle or *manubrium* (*m.*) and of a toothed head or *uncus* (*u.*). By means of the muscular walls of the chamber the heads of the mallei are worked backwards and forwards upon the forked uncus, and thus reduce the organisms taken as food to a fine state of division.

The pharynx leads by a short *gullet* into a spacious *stomach* (Fig. 267, *st.*) having a wall composed of very large epithelial cells, ciliated internally: with it are connected paired digestive glands. The stomach opens into a rounded *intestine* (*int.*), also ciliated internally, which communicates, by means of a short *cloaca* (*cl.*) with the exterior. The stomach and intestine are formed from the archenteron of the embryo and are therefore lined by endoderm:

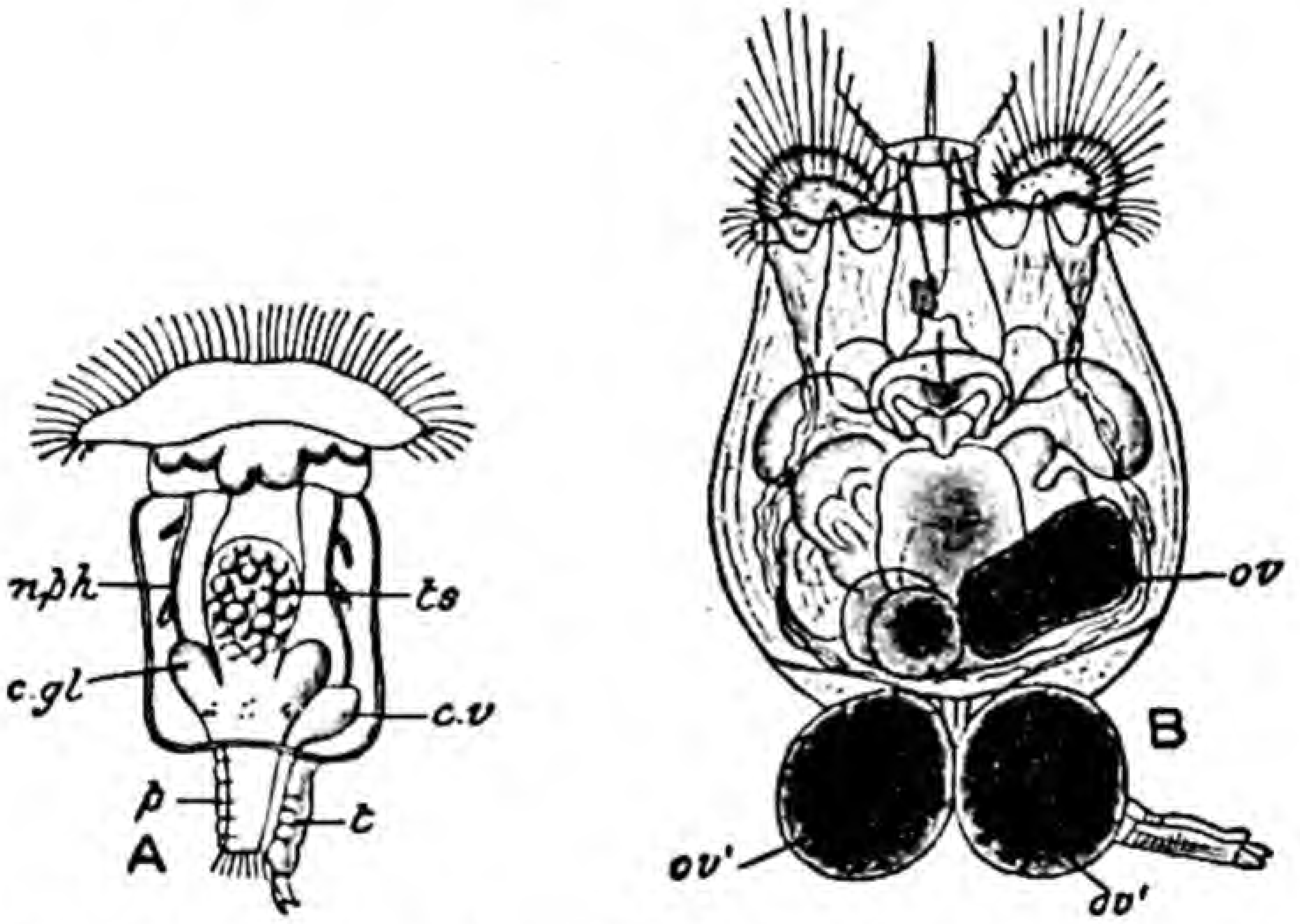


FIG. 266.—**Brachionus rubens.** *A*, male; *B*, female, with attached eggs. *c.gl.* cement-glands; *c. v.* contractile vesicle; *nph.* nephridial-tube; *ov.* ovum in body; *ov*[1]. ova attached to base of tail; *p.* penis; *t.* tail; *ts.* testis. (After Hudson and Gosse.)

the rest of the enteric epithelium is ectodermal, the pharynx being derived from the stomodæum, the cloaca from the proctodæum. Between the body-wall and the enteric canal is a spacious **body-cavity** containing a fluid which serves the purpose of blood and contains minute granules.

The **excretory system** consists of paired *nephridial tubes* (Figs. 264 and 267, *nph.*) resembling those of the Platyhelminthes. Their general direction is longitudinal, but they are a good deal coiled and give off little tag-like processes ending in flame-cells. Upon the end of each tag, projecting into the body-cavity, is a long flagellum. The lumen of the tubes is intra-cellular. Posteriorly the nephridial tubes open into a bladder or *contractile vesicle* (*c. v.*), the contents of which are discharged by periodical contractions, into the cloaca.

Nervous System and Sense-organs.—There is a single ganglion or *brain*

(Figs. 264 and 267, *br.*), of proportionally large size, situated at the anterior end of the body, above (dorsal to) the mouth and pharynx. On the dorsal surface of the brain, where it comes into contact with the body-wall, is a small red *eye-spot* (*e.*). The only other organs which can be considered as sensory are three structures known as *tactile rods* or *feelers*; one of these (*d. f.*) is a small cylindrical process tipped with stiff hair-like bodies, which projects from the dorsal surface just behind the trochal disc: the other two (*l. f.*) are paired, situated on the dorsal surface of the lorica and not prominent.

The tail contains a pair of *cement glands* (*c. gl.*), by the secretion of which the animal is able temporarily to attach itself.

Reproduction and Development.—The sexes are lodged in distinct individuals, which present a striking degree of sexual dimorphism. The preceding description applies to the female, which is the form most commonly met with.

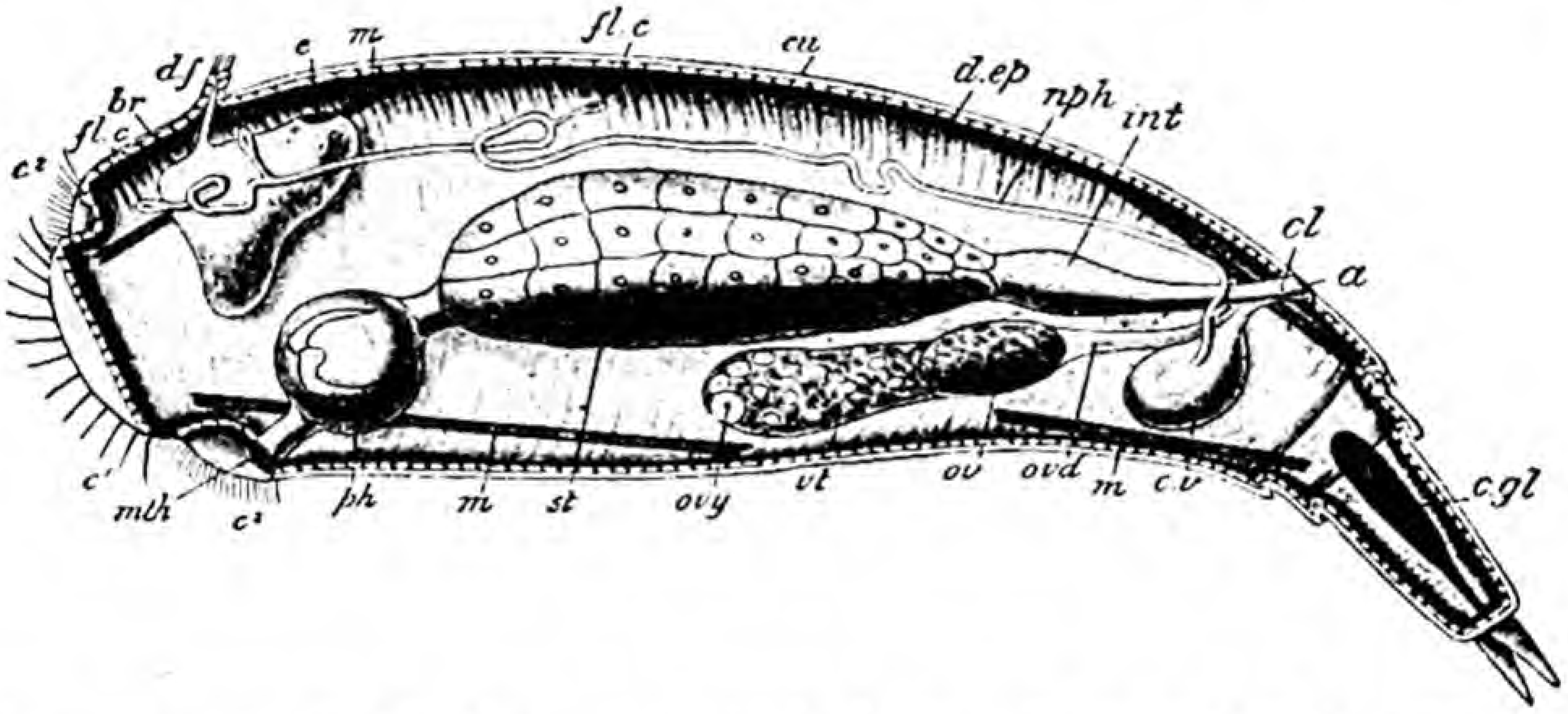


FIG. 267.—Diagram of a **Rotifer.** *a.* anus; *br.* brain; c^1. pre-oral, and c^2. post-oral circlet of cilia; *c.gl.* cement-gland; *cl.* cloaca; *cu.* cuticle; *c. v.* contractile vesicle; *d. ep.* deric epithelium; *d. f.* dorsal feeler; *e.* eye; *fl.c.* flame-cells; *int.* intestine; *m.* muscles; *mth.* mouth; *nph.* nephridial tube; *ov.* ovum; *ovd.* oviduct; *ovy.* germarium; *ph.* pharynx; *st.* stomach; *vt.* vitellarium.

In addition to the organs already mentioned, it has a *germarium* (*ov.*, *ovy.*), connected with a large *vitellarium* (*vt.*) and opening by an oviduct into the cloaca.

The male (Fig. 266, *A*) is a very minute creature, not more than one-fourth the size of the female, and is strangely degenerate in structure. The enteric canal is absent, the trochal disc simple in structure, the nervous system and nephridial tubes greatly reduced, and the greater part of the body occupied by a large testis (*ts.*) which opens by a duct at the extremity of a protrusible, dorsally placed penis (*p.*).

After extrusion the eggs are attached to the base of the tail of the female (*B*, *ov.*), where they undergo development: they are of two sizes, the larger giving rise to females, the smaller to males. Probably both kinds develop parthenogenetically, but in the autumn thick-shelled *winter eggs* are produced

which appear to require fertilization. These remain quiescent during the winter, and in the spring develop into females.

2. Distinctive Characters and Classification.

The Rotifera are animals of microscopic size. The anterior end is modified into a retractile trochal disc, with variously arranged cilia; the posterior end usually forms a mobile and often telescopically jointed tail. The mouth is anterior and more or less ventral in position, the pharynx contains a chitinous masticatory apparatus, and the anus is placed dorsally at the junction of the trunk with the tail. There is a spacious body-cavity devoid of epithelial lining. The excretory organs are a pair of nephridial tubes provided with flame-cells. The central nervous system consists of a single dorsal ganglion, with, in a few cases, a smaller ventral or sub-œsophageal ganglion. The sexes are separate, and the males are, in nearly all cases, smaller than the females and degenerate in structure.

The class is divided into four orders as follows :—*

Order 1.—Ploïma.

Rotifera in which locomotion is performed by the ciliated disc only; the tail, when present, is usually forked and more or less retractile; the trunk may or may not be covered by a lorica.

Examples: *Polyarthra, Hydatina, Asplanchna* (Fig. 269, *8, 7, 6*); *Trochosphæra, Pedalion, Hexarthra* (Fig. 270, *3, 1, 2*); *Brachionus*, Fig. 264; *Noteus, Notholca* (Fig. 269, *9, 10*).

Order 2.—Rhizota.

Rotifera which are fixed in the adult state by the truncated end of the non-retractile tail.

Examples: *Floscularia, Stephanoceros, Melicerta* (Fig. 269, *1, 2, 3*).

Order 3.—Bdelloïda.

Rotifera which both swim freely by means of the cilia of the disc and creep after the manner of a Leech; the tail is telescopic and forked distally.

Example: *Rotifer, Philodina* (Fig. 269, *5*).

Order 4.—Seisonida.

Marine parasitic Rotifers with the trochal disc reduced, the body long, narrow, and ringed, with a long slender neck-region, and an elongated foot provided at its extremity with a perforated disc.

Examples: *Paraseison* (Fig. 268).

3. General Organization.

External Characters.—The majority of the Rotifera are free-swimming, being propelled rapidly through the water by the action of the trochal disc.

* According to de Beauchamp (1909).

But in the Bdelloïda (Fig. 269, *5*), in addition to this mode of progression, the animal performs looping movements like those of a leech: the tail in this order is freely jointed, the various segments fitting into one another like the tubes of a telescope, and the body is fixed alternately by it and by the anterior end, the trochal disc being kept retracted while the animal moves in this way. Many of the Ploïma also have a telescopic tail, but in some, *e.g.*, *Asplanchna* (Fig. 269, *6*), this organ is absent. In *Pedalion* (Fig. 270, *1*) curious skipping movements are performed by the aid of six hollow limbs or appendages, one dorsal, one ventral, and two on each side. These curious organs are terminated by feathered setæ, and closely resemble the limbs of some of the lower Crustacea: each is moved by two opposing muscles which extend into its cavity (*1*, *B*, *m.*). Three pairs of similar appendages are present in *Hexarthra* (Fig. 270, *2*), the superficial resemblance of which to the *nauplius* larva of Crustacea is very striking; and four genera of unarmoured Ploïma, *e.g.*, *Polyarthra* (Fig. 269, *8*), possess simple or fringed setæ moved by muscles attached to their bases.

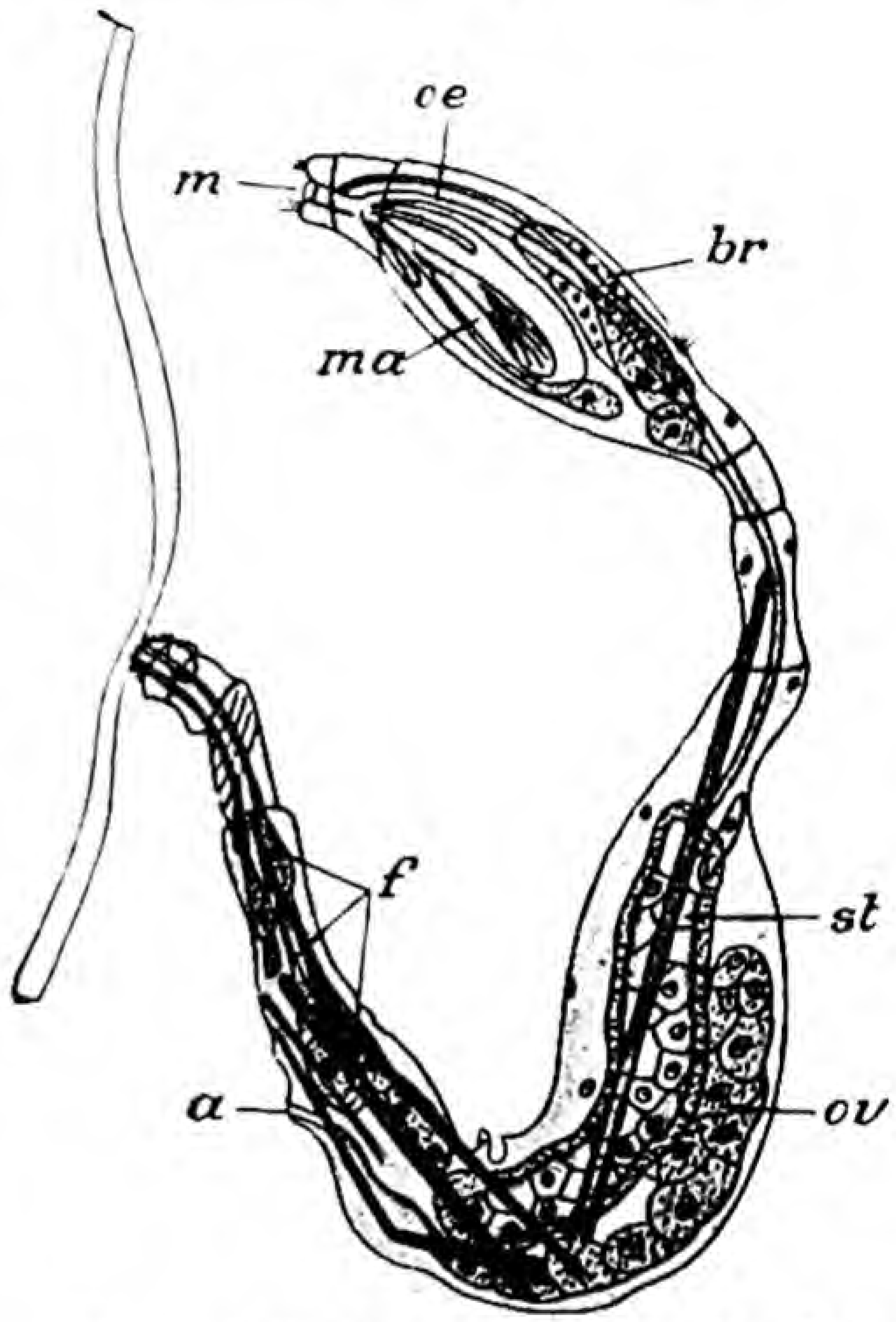


FIG. 268.—**Paraseison asplanchnus,** female, × 230. *a.* genital aperture; *br.* ganglion; *f.* foot-glands; *m.* mouth; *ma.* mastax; *oe.* œsophagus; *ov.* ovary; *st.* stomach. (After Plate.)

In the Rhizota the adult female is permanently fixed (Fig. 269, *1–4*). The end of the tail is devoid of the characteristic fork, and is attached to plants or other supports. Moreover the animal is surrounded by a tube into which it can retract itself completely, protruding the anterior end with the trochal disc when undisturbed. In most instances, as for example in *Floscularia* (*1*) and *Stephanoceros* (*2*), the tube is formed of a delicate, transparent, gelatinous secretion of the epidermis; but in *Melicerta* (*3*) it is built up of rounded pellets, which the animal moulds in a cup-like depression on the dorsal surface and places in position one by one. The pellets are usually formed of foreign particles, but in some species are made of the animal's own fæces.

The ciliation of the trochal disc is subject to considerable variation. In its simplest form the disc is surrounded by a single circlet of cilia, within which lies the mouth. A modification of this type may be produced by the prolongation of the ciliary crown into long arm-like processes fringed with cilia, as in *Stephanoceros* (*2*), or, as in *Floscularia* (*1*), into blunt elevations bearing

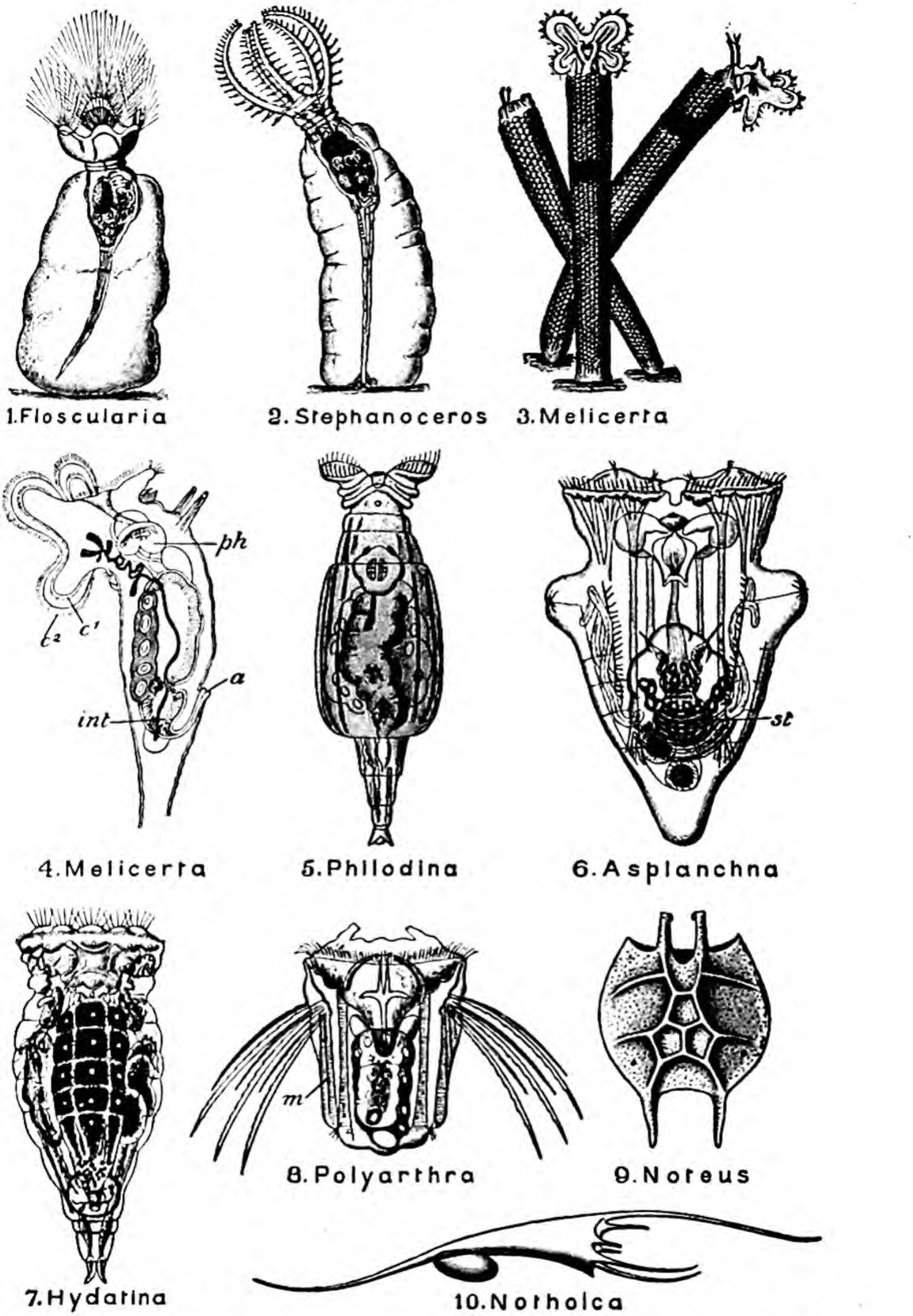


FIG. 269.—Typical forms of **Rotifera.**—*9* and *10* show the lorica only. *a.* anus; c^1. c^2. ciliary circlets; *int.* intestine; *m.* muscle; *ph.* pharynx; *st.* stomach. (After Hudson and Gosse.)

long stiff cilia like the pseudopodia of the Heliozoa. The single circlet may be folded upon itself, or a second type may be produced by the addition of a second circlet within and parallel to the first. The mouth in this case is always placed between the two circlets on the ventral side (Fig. 267), so that the inner

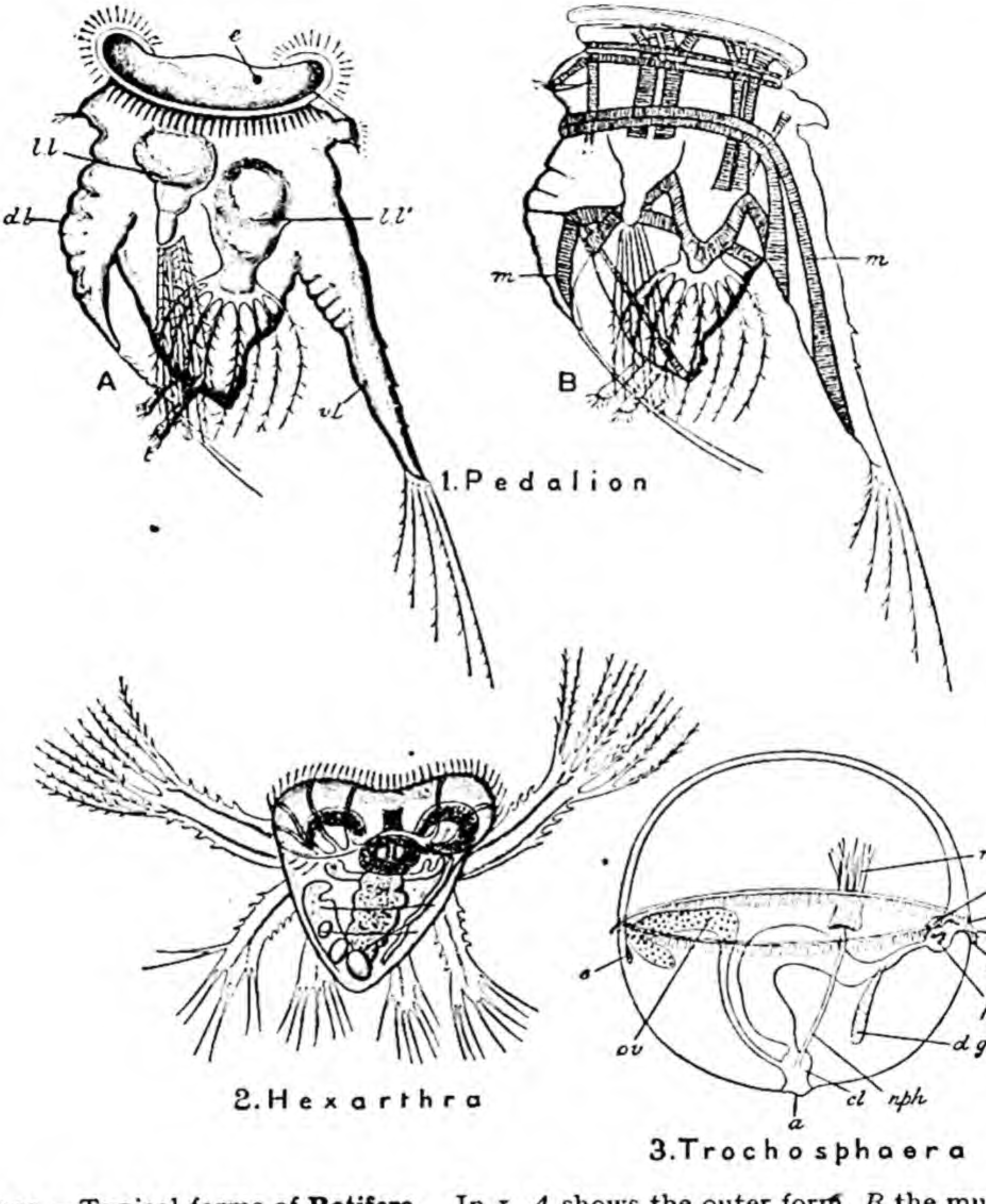


FIG. 270.—Typical forms of **Rotifera.** In *1*, *A* shows the outer form, *B* the muscular system. *a.* anus; *br.* brain; c^1., c^2. ciliary circlets; *cl.* cloaca; *d. gl.* digestive gland; *d. l.* dorsal limb; *e.* eye-spot; *l. l.*, *l. l'.* lateral limbs; *m.* muscles; *mth.* mouth; *nph.* nephridial tube; *ov.* ovary; *ph.* pharynx; *s.* sense-organ; *v. l.* ventral limb. (After Hudson and Gosse (*1* and *2*) and Korschelt and Heider (*3*).)

or anterior circlet is pre-oral and corresponds with the chief ciliary band of a trochophore larva, while the outer or posterior circlet corresponds with the postoral band found in many worm-larvæ. In the curious globular *Trochosphæra* (Fig. 270, *3*) there is a single equatorial circlet, which is pre-oral, and a few post-oral cilia: here the correspondence with the typical larva of the

Annelida, the Trochophora is singularly close. Lastly, both the pre- and post-oral circlets may be produced into more or less complex lobes, as in Melicerta (Fig. 269, *4*), or may be interrupted as in Brachionus, in which the pre-oral circlet is represented by three distinct lobes, or as in Pedalion, in which both circlets are divided into right and left halves. In one genus the trochal disc is absent.

Digestive Organs.—The typical form of mastax or pharyngeal mill is that described in Brachionus (Fig. 265). There is an unpaired *incus* consisting of a short stem or *fulcrum* (*f.*) and of two broad branches or *rami* (*r.*), and a pair of *mallei*, each consisting of a stout handle or *manubrium* (*m.*) and a broad, toothed head or *uncus* (*u.*). In some forms all the parts of the apparatus become very slender, the incus assuming the form of forceps (Fig. 271, *A*). Or the mallei may be absent and the two rami movable upon one another so as to convert the incus into a pair of forceps (*B*) used to seize prey, the mastax

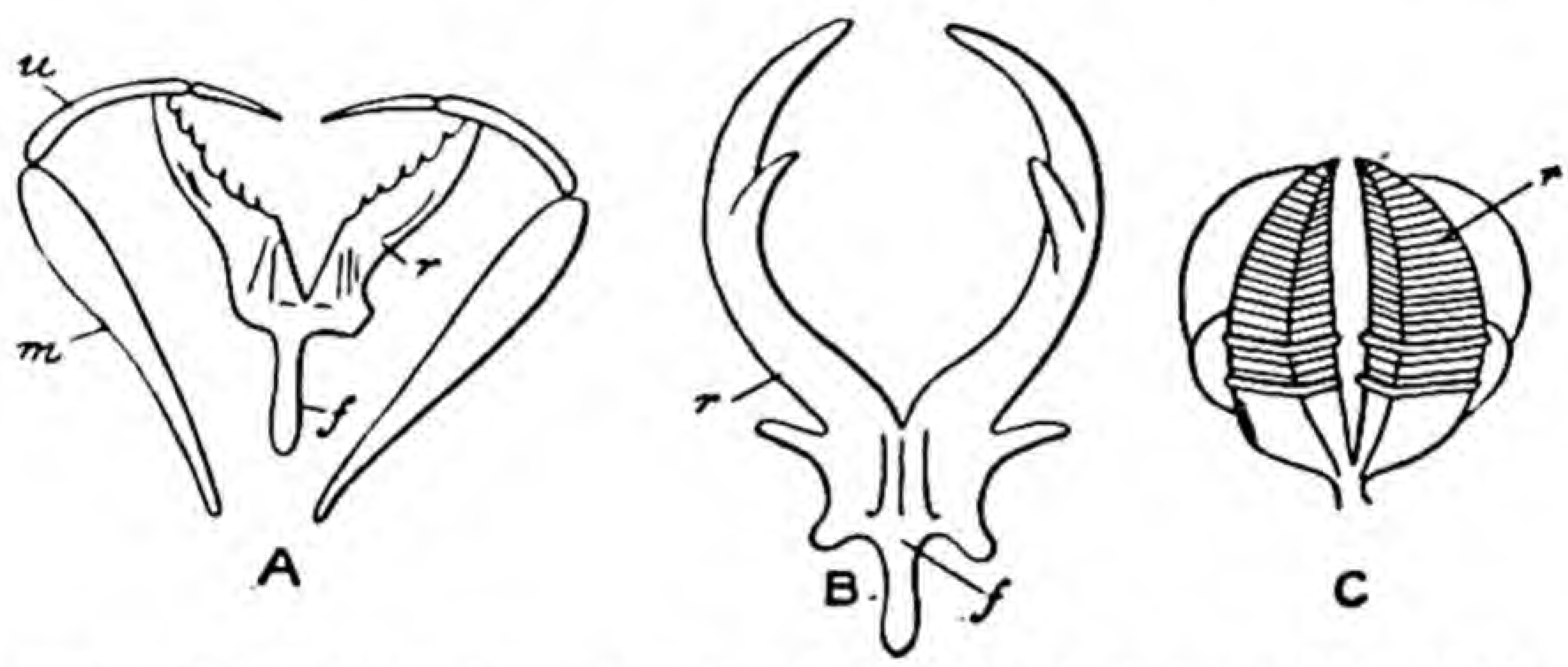


FIG. 271.—Typical forms of mastax. *A*, forcipate type; *B*, incudate type; *C*, ramate type; *f*. fulcrum; *m*. manubrium; *r*. ramus; *u*. uncus. (After Hudson and Gosse.)

being in this case protrusible. Lastly, the fulcrum and manubrium may be absent, and the unci and rami very strong and massive (*C*). Glands, supposed to be salivary, open into the mastax or œsophagus.

The *stomach* is always large, and usually has a pair of digestive glands opening into it: it may pass insensibly into the intestine, or the latter may be a distinct chamber of more or less globular form. In the Rhizota the intestine turns forwards so as to allow of the anus being brought over the edge of the tube in defæcation (Fig. 269, *4*, *a.*). In *Asplanchna* (*6*) the stomach ends blindly, the intestine, cloaca, and anus being absent.

The **excretory system** is very uniform in structure. It consists of a pair of more or less coiled nephridial tubes, placed longitudinally and giving off lateral branchlets which end in *flame-cells*. The outer surface of each flame-cell usually bears one or sometimes two flagella, which lie free in the body-cavity. Frequently, but not always, the two tubes open posteriorly into a contractile vesicle or bladder which discharges into the cloaca.

Nervous System and Sense-organs.—The nervous system usually consists of a single ganglion (Fig. 267, *br.*) towards the dorsal aspect of the anterior part of the body, and representing the brain or supra-œsophageal ganglion of the higher Worms: it sends nerves to the muscles, trochal disc, and tactile organs. In some cases a smaller ventral or sub-œsophageal ganglion is present as well, connected with the first by a pair of slender œsophageal connectives. Connected with the dorsal ganglion are a pair of lateral longitudinal nerves which run backwards to the tail, giving off branches in their course. One or more *eyes* (*e.*) are usually present in close relation with the brain, and are sometimes mere spots of pigment, but may be provided with a refractive body or lens. The only other sense-organs are the *tactile rods* (*d. f.*, *l. f.*), of which there is usually one on the dorsal surface near the anterior end of the body, and frequently two others, one on each side of the trunk. They are more or less rod-like structures, tipped with delicate sensory hairs and receiving nerves from the brain.

Reproduction and Development.—In most cases the female reproductive organs have the same general character as in Brachionus, *i.e.*, the gonad is unpaired (Fig. 264), consists of germarium and vitellarium, and is provided with an oviduct (Fig. 267). But in some of the Bdelloïda, such as *Philodina*, there are two ovaries, not divisible into germ-gland and yolk-gland, and the oviduct is absent. The males are smaller than the females and degenerate in structure, the enteric canal being atrophied (Fig. 266, *A*). There is a large testis (*t.*) with a duct opening at the end of a protrusible penis (*p.*), which is dorsal in all but *Asplanchna*, in which it, as well as the cloacal opening of the female, appears to be ventral. Apparently *hypodermic impregnation* sometimes takes place, *i.e.*, the body-wall of the female may be perforated at any place for the entrance of the sperms.

Three kinds of eggs are produced: large and small *summer eggs*, which always develop parthenogenetically, the larger giving rise to females, the smaller to males; and thick-shelled *winter eggs*, which require fertilization, and remain in an inert condition all through the winter, finally developing in the spring. Most Rotifers are oviparous, but some (*Philodina*, etc.) bring forth living young, which are born by breaking through the body-wall or through the cloaca, thus causing the death of the parent.

Cleavage is total and irregular, the fertilized ovum dividing into macromeres and micromeres. An epibolic gastrula is formed, the blastopore closes, and invaginations of ectoderm give rise to the stomodæum and proctodæum. The tail is formed as a prolongation of the postero-ventral region of the embryo, and contains at first an extension of the endoderm. No metamorphosis is known to take place in any member of the class.

Mode of Life.—A few Rotifers live in the sea, but the majority are fresh-water forms, occurring in lakes, streams, ponds, and even in puddles the water

of which is rendered foul and opaque by mud and sewage. Frequently the water in which they live is dried up, and the thick-shelled winter eggs may then be widely dispersed by wind. It is even stated that the adult animals may survive prolonged desiccation and resume active life when again placed in water. They are able to survive prolonged exposure to temperatures far

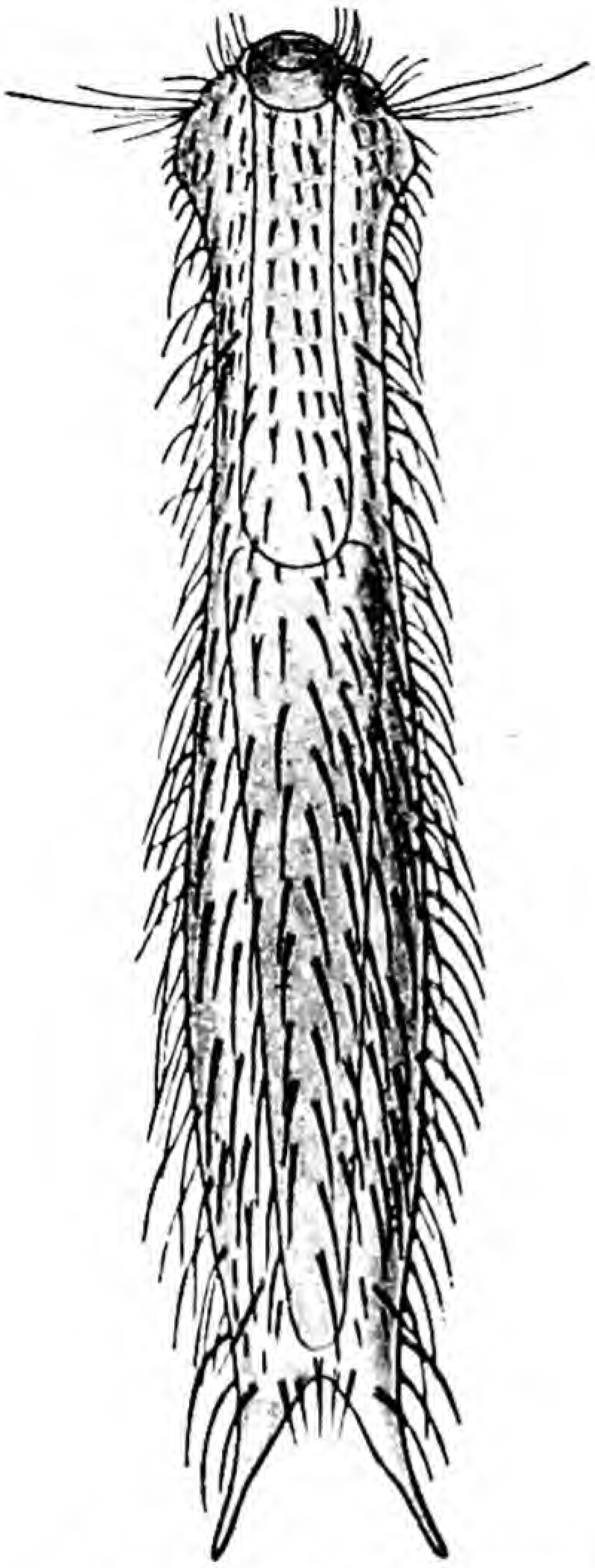


FIG. 272.—**Chaetonotus maximus.** Highly magnified. (After Zelinka.)

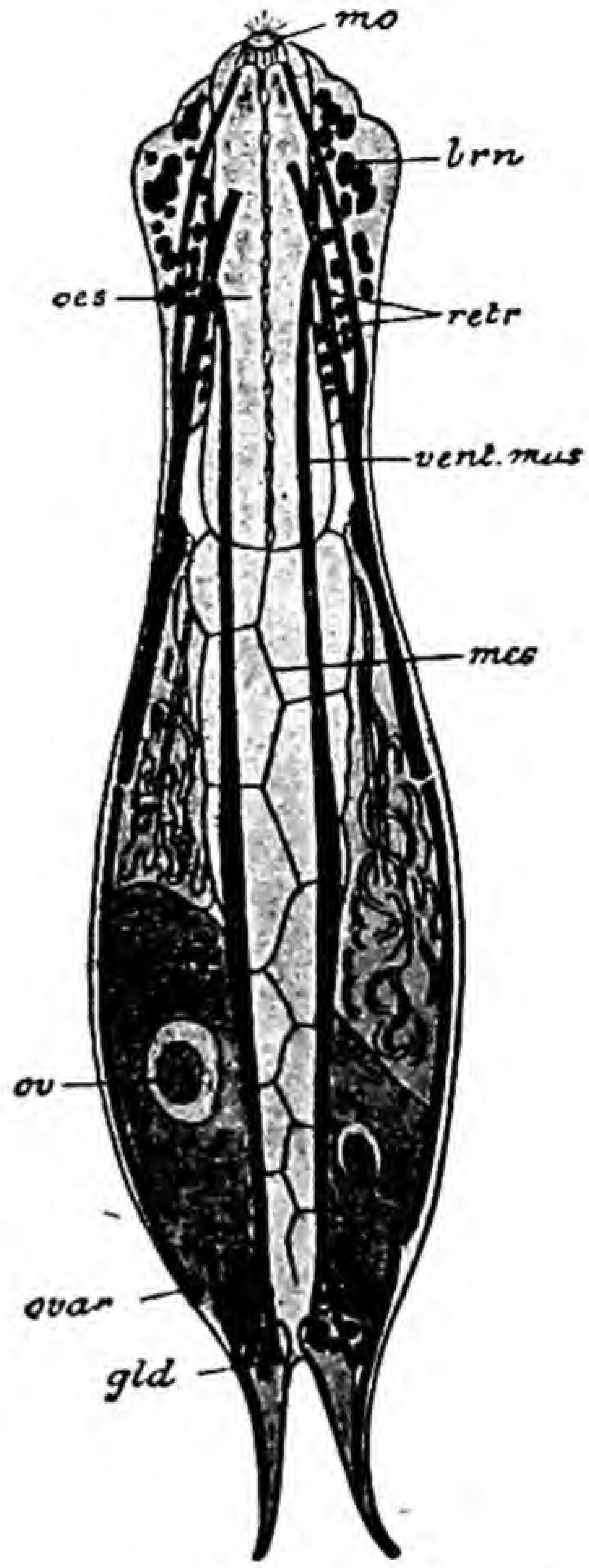


FIG. 273.—**Chaetonotus maximus** (organization). *brn.* brain; *gld.* adhesive gland; *mes.* mesenteron; *mo.* mouth; *œs.* œsophagus; *ov.* ovum; *ovar.* ovary; *retr.* retractor muscles; *vent. mus.* ventral muscle. (After Zelinka.)

below the freezing point of water. Many forms cling to the bodies of higher animals in order to obtain a share of their food, thus leading a kind of commensal existence. Others go a step further and become true external parasites, like *Drilophaga* on a fresh-water Oligochæte (*vide* Section VII), or *Seison* on the little Crustacean *Nebalia*. Others, again, are internal parasites, such as *Albertia* in the cœlome of Earthworms and the intestine of fresh-water Oligo-

chætes (*Nais*), and *Notommata werneckii* in the cells of the fresh-water Alga *Vaucheria*.

Affinities.—The affinities of the Rotifera are very obscure. Their general resemblance to the free-swimming larvæ of Annelids (phylum *Annelida*) is extremely close, and, in particular, the curious *Trochosphæra* is, to all intents and purposes, a sexually mature trochophore (cf. Section VII) with a mastax. The excretory organs recall those of the Platyhelminthes.

APPENDIX TO THE ROTIFERA.

THE GASTROTRICHA.

The *Gastrotricha* (Figs. 272 and 273) are a small group of minute fresh-water animals which are allied, though certainly not very closely, to the *Rotifera*. The body is spindle-shaped with flattened ventral surface. The ventral surface bears two longitudinal bands of cilia; the dorsal is non-ciliated, but in some forms bears a number of longitudinal rows of slender, pointed, cuticular processes. The aboral end is narrow and usually bifurcated.

On the head are four tufts of flagella, which are partly sensory, partly vibratile. The mouth, situated at the anterior end, leads by a narrow tube into the thick-walled œsophagus. At the beginning of the latter are a number of small chitinous denticles, and in front of them a circlet of setæ. The œsophagus leads to a wide elongated stomach followed by a short intestine which terminates in an anal aperture at the posterior extremity. The excretory organs are a pair of unbranched coiled tubes each opening on the ventral surface and terminating internally in a flame-cell. The nervous system consists of a large dorsally and anteriorly situated cerebral ganglion or brain giving off a pair of ventro-lateral longitudinal nerves. The sexes are mostly united, and there is no metamorphosis.

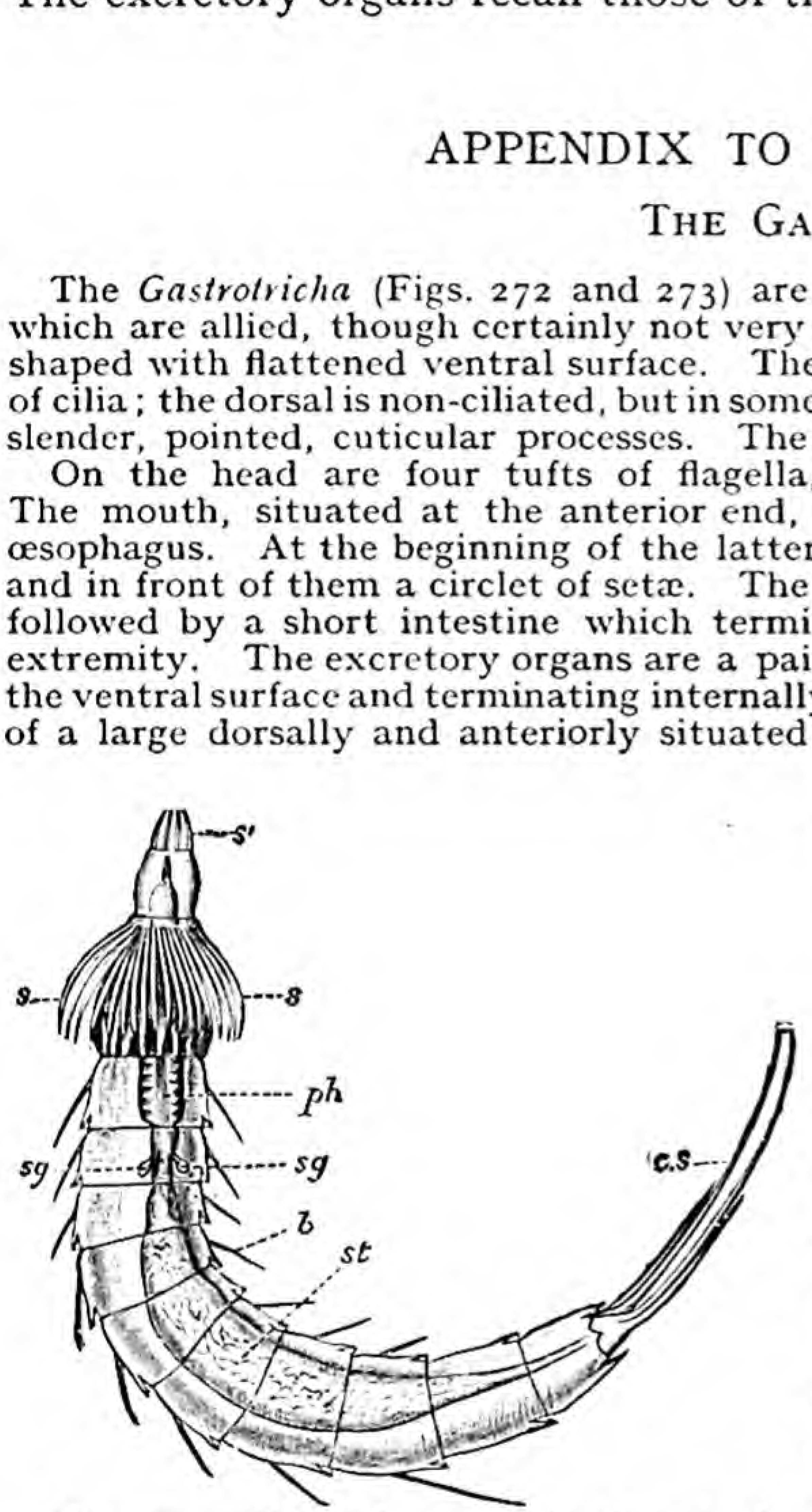


FIG. 274.—**Echinoderes,** × about 210. *b.* spine; *c. s.* caudal spine; *ph.* pharynx; *s.* and *s'.* spines on the proboscis; *s. g.* salivary glands; *st.* stomach. (After Hartog.)

THE KINORHYNCHA (ECHINODERIDÆ).

Echinoderes is a minute marine worm of cylindrical form with a flattened ventral surface. The body is segmented, or divided into rings, eleven or twelve in number, all strongly cuticularized, and most of them bearing spines (Fig. 274). The mouth is placed at the anterior, the anus at the posterior end of the body: the former opens into a sac, which can be everted so as to form a proboscis or *introvert*, and is armed with spines. The enteric canal consists of a muscular pharynx and a straight intestine. The excretory organs are a pair of sacs, beginning with a flame-cell with a single cilium and opening by ciliated ducts on the tenth segment. The sexes are separate: the gonads are paired sacs opening at the posterior end of the body.

THE CALYSSOZOA (ENDOPROCTA).

The Calyssozoa are a group of small sedentary animals which are either solitary or colonial. In their external features they recall the Hydroidea amongst the Cœlenterata. In view of certain superficial similarities, they were formerly included among the *Bryozoa* (Section X), along with the cœlomate *Ectoprocta*, with which they are, however, not related. The Calyssozoa

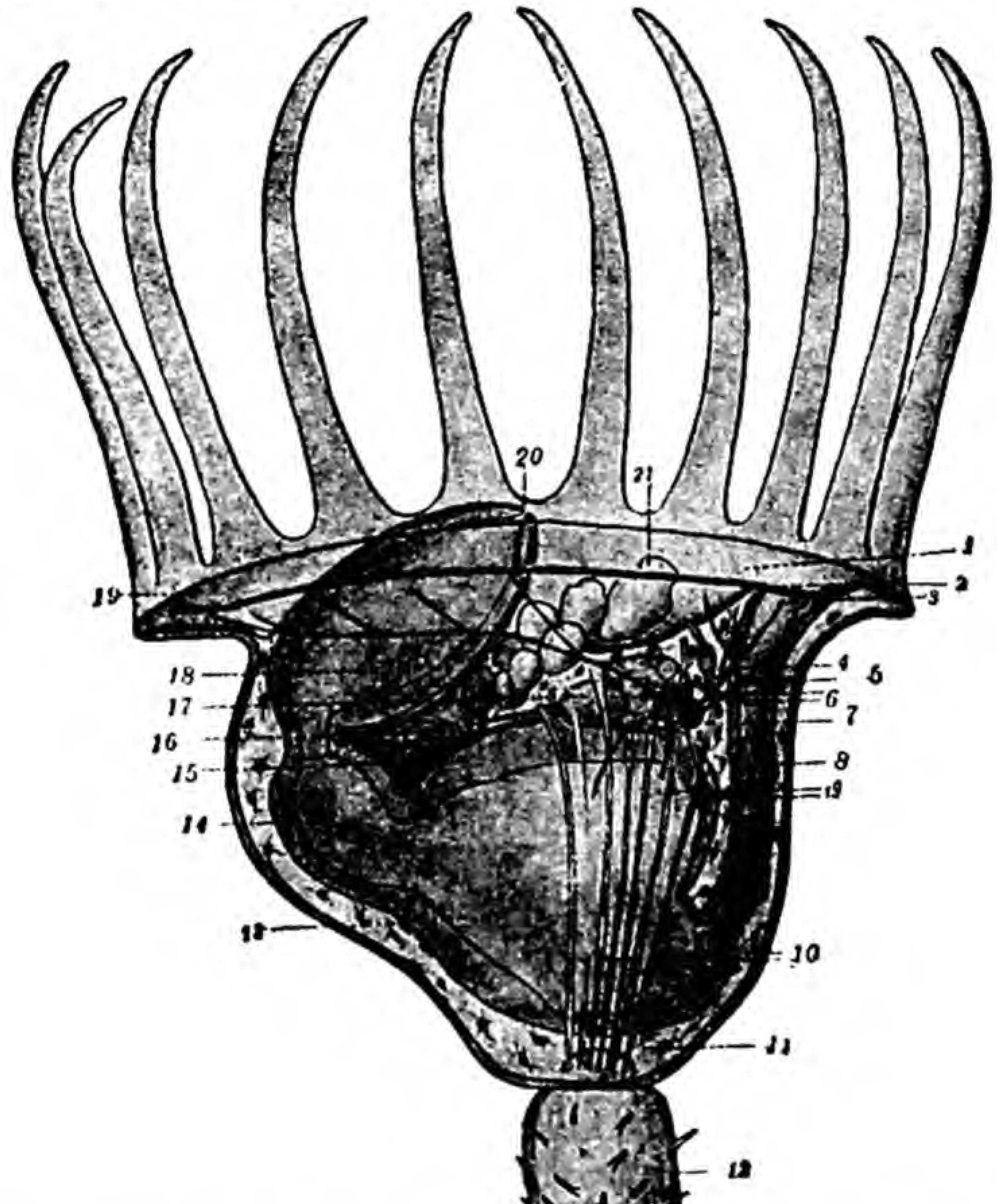


FIG. 275.—**Pedicellina cernua (Pallas).** Lateral aspect of calyx. 1, ciliated groove; 2, lower lip; 3, mouth; 4, excretory tube; 5, ovary; 6, tentacular nerves; 7, sub-œsophageal ganglion; 8, œsophagus; 9, muscles; 10, retractor muscles of vestibule; 11, body-cavity; 12, stalk; 13, stomach; 14, intestine; 15, brood space; 16, genital pore; 17, testis; 18, rectum; 19, rim of calyx; 20, anus; 21, larva. (From Kükenthal's *Handbuch der Zoologie* (Walter de Gruyter & Co.), original Cori.)

include the genera *Pedicellina* (Fig. 275), *Loxosoma*, *Urnatella*, *Myosoma*, *Gonypodaria* and *Ascopodaria*, with one or two other less completely known forms. They are all marine except Urnatella—an American fresh-water genus.

The body is *cup-shaped*, with a circlet of tentacles and a stalk. The rim of the cup (*calyx*) can be inverted over a cavity—the *vestibule*—within which the tentacles can be withdrawn, and which contains both mouth and anus. An *epistome* overhangs the mouth. The space between the alimentary canal and the wall of the body is filled, more or less completely, with parenchyma.

A pair of excretory organs are present. In Loxosoma they lie one on either side of the œsophagus and open separately on the exterior; they are ciliated intra-cellular tubes, each of which probably begins in a flame cell. In Urnatella the two excretory tubes unite to open into the *cloaca*—a diverticulum of the vestibule. The *ganglion* (Fig. 275, 7), is bilobed in Loxosoma. *Testes* and *ovaries* occur in the same individual in some, but appear to mature at different times: they are provided with special ducts; in others the sexes are separate.

Pedicellina and Urnatella are colonial, Loxosoma solitary. In Pedicellina (Fig. 275) there is a creeping stolon with which a number of zooids are connected; a diaphragm separates the body of each zooid from the stalk. *Gonypodaria ramosa* has a branching stalk. Urnatella has a disc of attachment with one to six, jointed, branching stems. In Loxosoma, which is found attached to various annelid worms, two parts are distinguishable—the calyx or *body* and the *stalk*. In the base of the latter is the so-called *foot-gland*, consisting of a small number of granular cells arranged around a central space opening on the exterior. Buds are formed, but become detached before reaching maturity. Cleavage of the ovum is complete, and a gastrula is formed by invagination.

The ciliated larva, after a period of free-swimming existence, becomes attached by the oral surface—the vestibule, mouth, and anus directed downwards. Very soon a rotation is observed to take place, by virtue of which the vestibule and developing tentacles, with the mouth and anus, become carried to their permanent position on the free surface of the animal.

SECTION VII

PHYLUM ANNELIDA

The phylum Annelida comprises three classes of worms: the *Chætopoda* (marine *Polychæta*, terrestrial and fresh-water *Oligochæta*), the *Hirudinea* or *Leeches*, and the *Archiannelida*. In close connection with these the *Echiurida* and *Sipunculida* will also be described in this section. The Annelida in general have the elongated body divided externally into a number of rings, which represent a division of the internal parts into a series of segments or metameres. The body cavity is a *true cœlome* which lies between layers of mesoderm. A system of blood vessels is present in most Annelida. The nervous system consists in most cases of a cerebral ganglion, œsophageal connectives, and a double ventral nerve-cord, which is segmented into a series of ganglia. The organs of excretion are in the form of metamerically arranged pairs of tubes, the *nephridia* or *segmental organs*, closed internally or leading from the cœlome to the exterior; and united with these, or distinct from them, is a series of paired ducts, the *cœlomoducts*, for the passage outwards of the reproductive elements.

CLASS I.—CHÆTOPODA.

The Chætopoda, comprising the Earthworms, Fresh-water Worms, and Marine Annelids, are Worms the body of which, unlike that of a Flat-worm or a Round-worm, is made up of a series of more or less completely similar segments or *metameres*, each containing a chamber or compartment of the body-cavity and a section of the alimentary canal and other organs. At the sides of each are typically a pair of muscular processes, the *parapodia*, which do duty as limbs, bearing bundles of *setæ* (*chætæ*) or bristles, and usually also certain tactile appendages, the *cirri*. There is an extensive cœlome, incompletely divided into a series of chambers corresponding to the segments by a series of muscular partitions which act also as mesenteries, being attached internally to the alimentary canal. The latter extends throughout the length of the body; the intestine is usually constricted, the constrictions being either segmental, *i.e.* opposite the middle of the segments, or inter-segmental, *i.e.* opposite the intervals between the segments. There is a well-developed blood-vascular system in the majority of the Chætopoda, and organs of respiration in the shape of gills or branchiæ are usually developed. The excretory organs are in the form of segmentally arranged pairs of tubes, the *nephridia*. The

nervous system consists of a bilateral principal ganglion or brain situated in the prostomium, and a double chain of ganglia extending throughout the body. The sexes are in some distinct, in others united. When a definite larval form occurs it is a so-called *trochophore*.

The general shape of a typical trochophore is oval or pear-like (Fig. 276) with a broader and a narrower end and distinct bilateral symmetry. Encircling the body about the middle, or rather nearer the broad than the narrow end, is a double circlet of strong cilia, the *pre-oral circlet* (*Wkr.*) or *prototroch*, situated on a corresponding ring-like thickening of the ectoderm; behind the mouth is often a second circlet of cilia, the *post-oral circlet* (*wkr.*), and a ciliated groove or ciliated streak usually runs backwards from it along the middle of the ventral surface. The mouth, situated just behind the pre-oral circlet, leads into an alimentary canal, which at first runs nearly transversely, and then bends round so as to extend back towards the narrow end, near which it opens on the exterior by an anal aperture. About the middle of the broader (anterior) end of the trochophore is a thickening, the *apical plate* (*SP.*), projecting from which are usually a number of sensory cilia (*WS.*); and in many trochophores eye-spots and a pair of short tentacles occur in close relation with the apical plate, which is the nerve centre of the larva. A pair of tubes—the excretory organs (*Neph.*)—may be present.

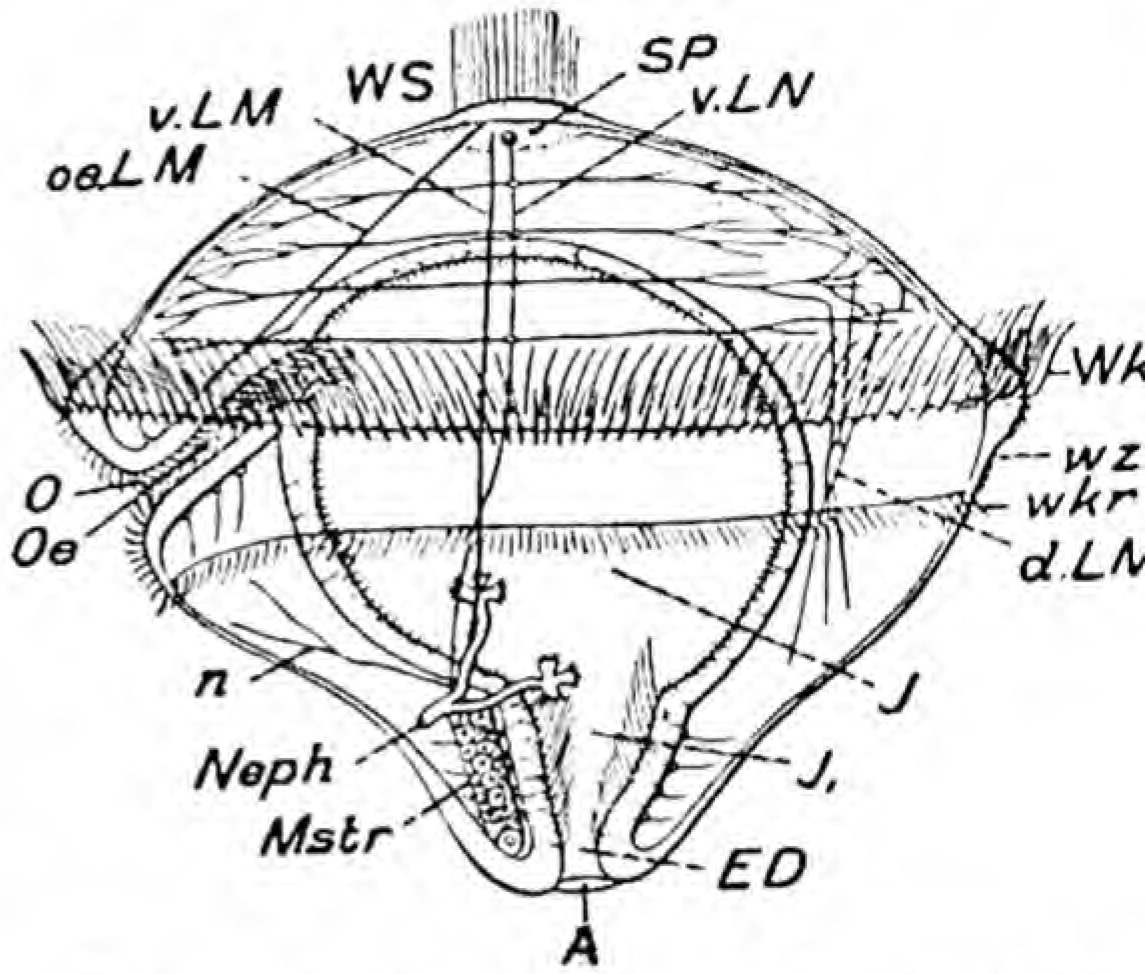


FIG. 276.—**Trochophore.** *A.* anus; *d.LM.* dorsal muscles; *ED.* rectum; *J.* stomach; *J*[1]. intestine; *Mstr.* mesoderm-band; *n.* nerves; *Neph.* excretory organs; *O.* mouth; *Oe.* œsophagus; *œLM.* œsophageal longitudinal muscle; *SP.* apical plate; *v.LM.* ventral muscle; *v.LN.* lateral nerve; *Wkr.*, *wkr.*, pre- and post-oral bands of cilia; *WS.* apical cilia; *wz.* adoral cilia. (From Hertwig's *Zoology*, after Hatschek.)

I. EXAMPLES OF THE CLASS.

a. Nereis dumerilii.[1]

General External Features.—Various species of *Nereis* occur abundantly between tide-marks on the sea-shore, under stones, and among sea-weed, in all parts of the world. The worm varies considerably in colour even in the same species, the differences being partly due to differences in the stage

[1] Though *Nereis dumerilii* is here named as the example, and the majority of the figures refer specially to that species, the description given would apply almost equally well to a considerable number of species of the genus.

of development of the sexual elements. In *N. dumerilii* the prevailing colour is some shade of violet, with a blush of red in the more vascular parts due to the bright red colour of the blood. In shape (Fig. 277) the body, which may be about 7 or 8 centimetres in length, is long and narrow, approximately cylindrical, somewhat narrower towards the posterior end. A very distinct *head*, bearing eyes and tentacles, is recognizable at the anterior end; the rest is divided by a series of ring-like narrow grooves into a corresponding series of *segments* or *metameres*, which are about eighty in number altogether; and each of these bears laterally a pair of movable muscular processes called the *parapodia*, provided with bundles of bristles or *setæ* (*chætæ*). The head (Fig. 281) consists of two parts, the *prostomium* (*præst.*) and the *peristomium* (*perist.*). The former bears on its dorsal surface four large rounded *eyes*, in front a pair of short cylindrical *tentacles* (*tent.*), and further back a pair of somewhat longer stout appendages or *palpi* (*palp.*). The *peristomium*, which has some resemblance to the segments of the body, though wanting the parapodia, bears laterally four pairs of long, slender, cylindrical tentacles (*perist. tent.*): on its ventral aspect is a transversely elongated aperture, the *mouth*. The segments of the body differ little in external characters from one another throughout the length of the worm. Each bears laterally a pair of parapodia, which in the living animal are usually in active movement, aiding in creeping, or acting as a series of oars for propelling it through the water. When one of the parapodia (Fig. 278) is examined more attentively it is found to be *biramous*, or to consist of two distinct divisions—a dorsal, which is termed the *notopodium* (*noto*), and a ventral, which is called the *neuropodium* (*neuro*). Each of these is further subdivided into several lobes, and each bears a bundle of setæ. Each of the bundles of setæ is lodged in a sac formed by invagination of the epidermis—the *setigerous sac*—and is capable of being protruded or retracted and turned in various directions by strands of muscular

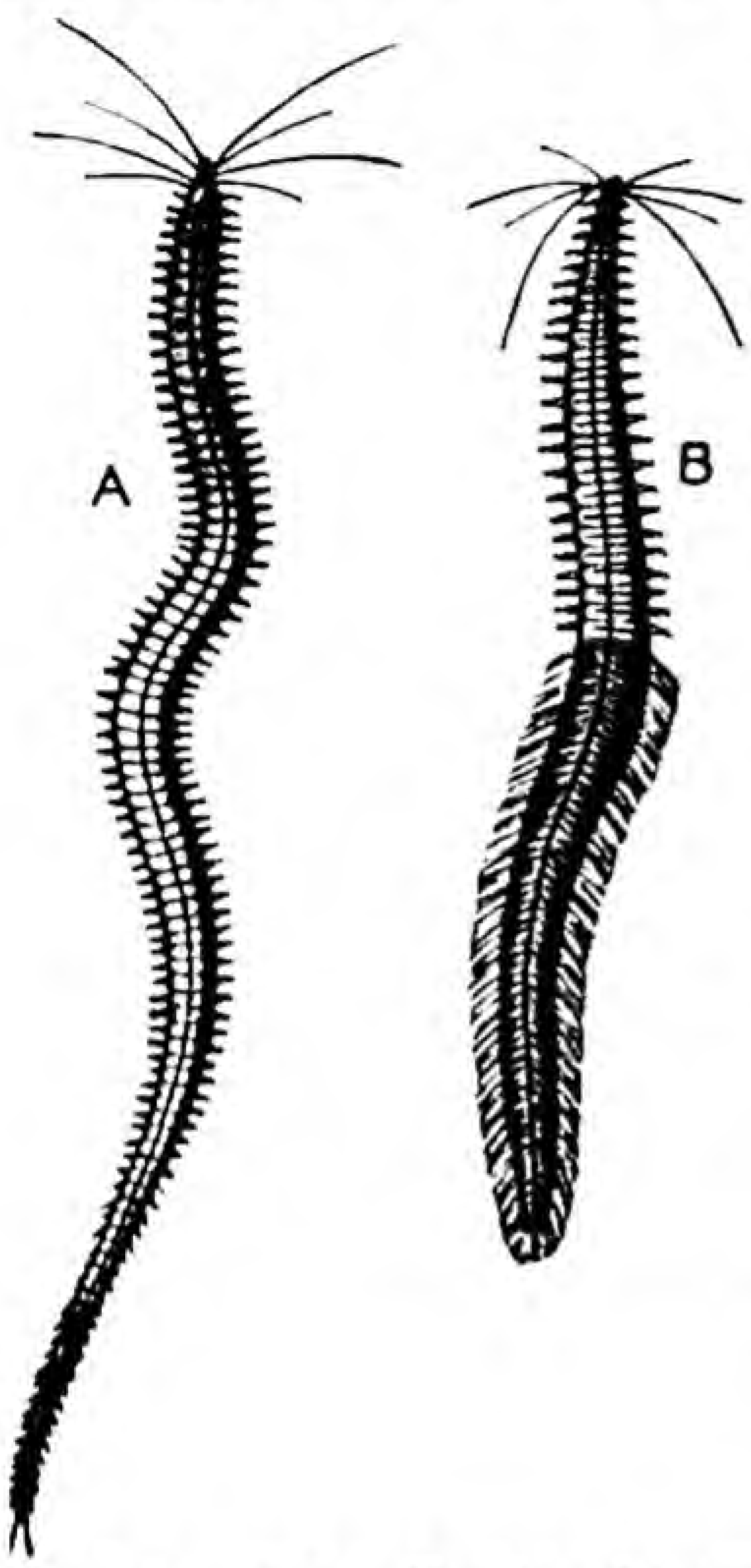


FIG. 277.—**Nereis dumerilii**, natural size. *A*, *Nereis* phase; *B*, *Heteronereis* phase. (After Claparède.)

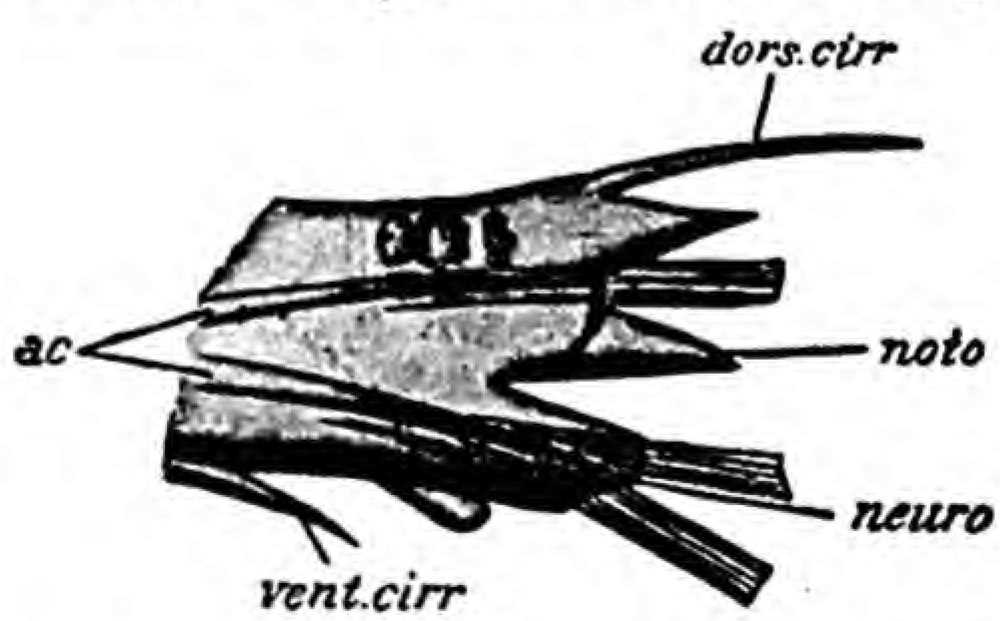


FIG. 278.—**Nereis dumerilii.** A single parapodium, magnified: *ac.* aciculum; *dors. cirr.* dorsal cirrus: *neuro.* neuropodium; *noto.* notopodium; *vent. cirr.* ventral cirrus. (After Claparède.)

fibres in the interior of the parapodium. In each bundle there is, in addition to the ordinary setæ, a stouter, straight dark-coloured seta (*ac.*), the pointed apex of which projects only a short distance on the surface; this is termed the *aciculum*. The ordinary setæ (Fig. 279) are exceedingly fine, but stiffish, chitinous rods, of which two principal kinds are recognizable: both have a terminal *blade* articulating with the main *shaft* of the seta by a distinct joint, but in the one variety the shaft of the seta is finer than in the other, and the terminal blade long, slender, and nearly straight, whereas in the other variety it is short and slightly hooked. On the dorsal side of the parapodium is a short cylindrical, tentacle-like appendage, the *dorsal cirrus* (Fig. 278, *dors. cirr.*), and a similar, somewhat shorter appendage, the *ventral cirrus* (*vent. cirr.*), is situated on its ventral side. The last segment of the body, the *anal segment*, bears posteriorly a small rounded aperture, the *anus*; this segment is devoid of parapodia, but bears a pair of appendages, the *anal cirri*, similar in character to the cirri of the ordinary segments, but considerably longer.

FIG. 279.—**Nereis dumerilii.** Setæ highly magnified. (After Claparède.)

On the ventral surface, near the bases of the parapodia, there is in each segment a pair of very fine apertures, the openings of the nephridia.

The **enteric canal** is a straight tube running throughout the length of the body from the mouth to the anus. Between the outer surface of this tube and the inner surface of the wall of the body is a considerable space—the **cœlome**, *body-cavity*, or *perivisceral cavity*—filled with a fluid, the *cœlomic fluid*, containing amœboid corpuscles. The walls of the cœlome (Fig. 282) are lined with a thin membrane, the *peritoneum* or *cœlomic epithelium*, of which the outer layer—that lining the body-wall—is the *parietal* layer (*par. peri.*), that covering the outer surface of the alimentary canal the *splanchnic* or *visceral* layer (*visc. peri.*). The space is divided by a series of transverse partitions or *septa* passing inwards from the body-wall to the wall of the alimentary canal opposite the grooves between the segments, and thus dividing the cœlome into a series of chambers, each of which corresponds to one of the segments. These partitions are not complete, spaces being left around the alimentary canal and elsewhere through which neighbouring chambers communicate.

The mouth leads into a wide cavity, the *buccal cavity*, continued back into a *pharynx* (Fig. 281, *ph.*). These two chambers extend through the peristomium and the first to the fourth segments of the body. They are lined with a tolerably thick cuticle, continuous with a similar layer lining the outer surface

of the body, and in the buccal cavity are a number of very small dark brown chitinous *denticles*, which are very regularly arranged. The posterior part of the pharynx (*dentary region*) has very thick walls composed of bundles of muscular fibres, which are concerned in the movements of a pair of laterally placed chitinous *jaws*. Each jaw is elongated in the direction of the long axis of the body, rounded at the posterior end or base where it is embedded in muscle, pointed at the apex, which is strongly incurved; the inner edge is divided into a number of strong serrations or teeth: the whole jaw might be compared to a pruning-hook with its cutting edge deeply serrated (Fig. 280, *B*).

Behind the pharynx the alimentary canal narrows considerably to form a tube, the *œsophagus* (*œs.*), which runs through about five segments to open into the intestine.

Running backwards and inwards from the wall of the peristomium to the wall of the buccal cavity and pharynx are a number of bands or sheets of

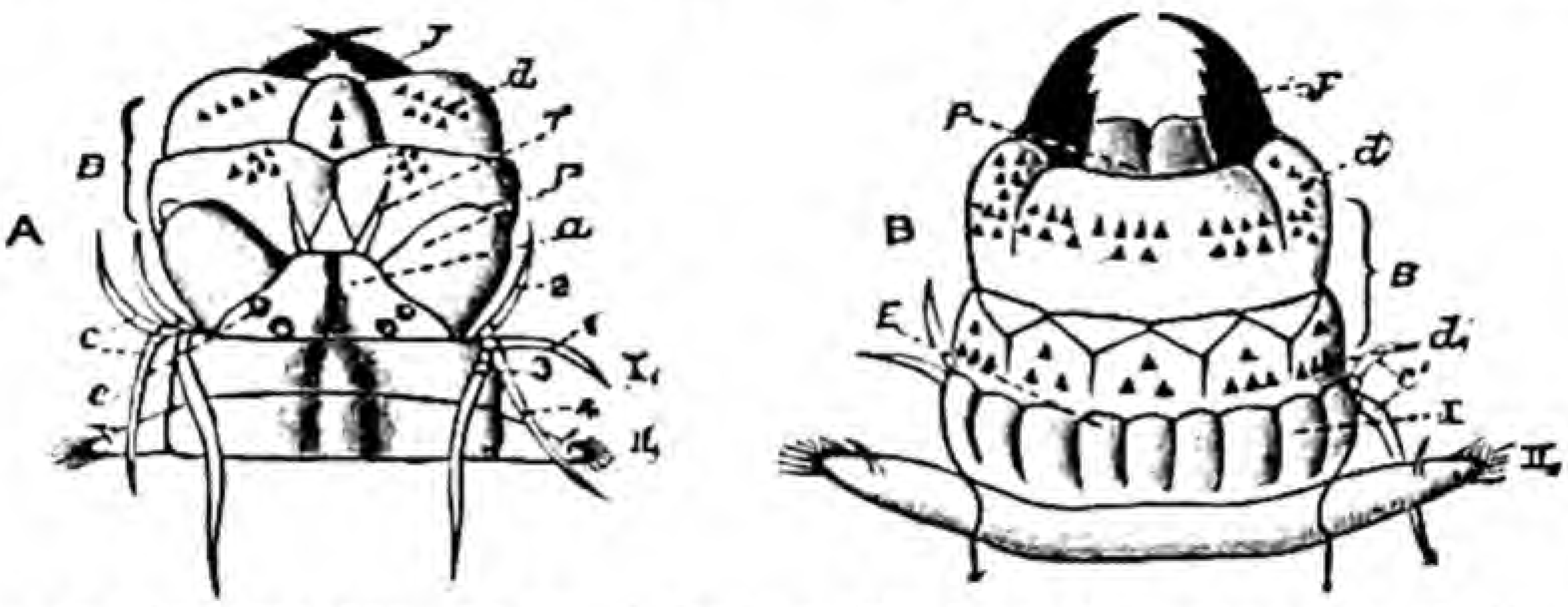


FIG. 280.—**Nereis diversicolor,** × 4. Head with buccal region everted. **A,** dorsal view; **B,** ventral view. *a*, prostomium; *B*, everted buccal region; *c, c'*, peristomial tentacles, 1, 2, 3, 4; *d*, denticles; *e*, eyes; *E*, lower lip; *P*. palp in **A**, entrance to pharynx in **B**; *J*, jaw; *T*, prostomial tentacle; *I*, peristomium; *II*, parapodium of first body-segment. (From the *Cambridge Natural History*.)

muscle, the *protractor muscles*, by the contraction of which, and the pressure of the cœlomic fluid, this anterior part of the alimentary canal can be everted so as to form a *proboscis* (Fig. 280), and thus the jaws are thrust forth and rendered capable of being brought to bear on some small living animal or fragment of animal matter, to be seized and swallowed as food. The eversion is arrested at a certain point by means of a muscular diaphragm passing from the wall of the buccal cavity to that of the first body-segment. The proboscis is withdrawn again by a *retractor* sheet of muscle, which passes inwards and forwards to be inserted into the wall of the alimentary canal at the junction of the pharynx and œsophagus.

Into the œsophagus open a pair of large unbranched glandular pouches, or *cœca* (Fig. 281, *gl.*), which probably are of the nature of digestive glands. The *intestine* (*int.*) is a straight tube of nearly uniform character throughout, regularly constricted in each segment—the constrictions becoming much deeper towards the posterior end of the body. The part of the intestine which lies in the last segment is termed the *rectum*.

The wall of the alimentary canal (Fig. 282) consists (1) of the visceral layer of the cœlomic epithelium (*visc. peri.*); (2) of a layer of longitudinal muscular fibres (*long. mus.*); (3) of a layer of circular muscular fibres (*circ. mus.*); and (4) of the enteric epithelium (*ent. ep.*), consisting of close-set, long, narrow cells. To these layers is superadded in the buccal cavity and the pharynx an internal chitinous cuticle, continuous with that of the general outer surface.

Developmentally the buccal cavity and the pharynx constitute the *stomodæum*, the rectum the *proctodæum*, the rest of the alimentary canal the *mesenteron*.

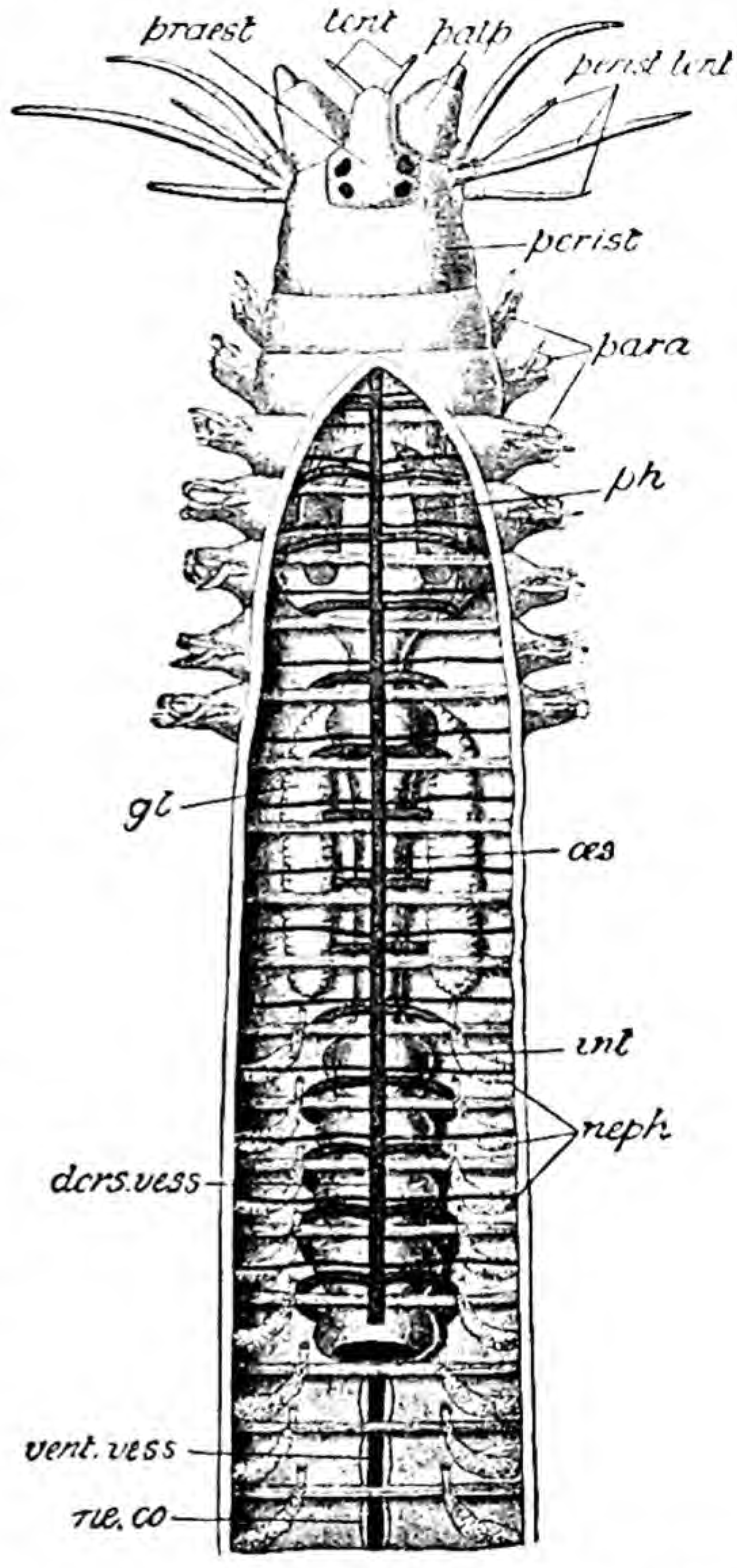


FIG. 281.—**Nereis dumerilii.** Semi-diagrammatic view of the anterior portion of the body with the dorsal body-wall removed, so as to show the alimentary canal, the septa, the blood-vessels, and the nephridia; a portion of the intestine removed so as to show the ventral blood-vessel and nerve-cord which lie below. *dors. vess.* dorsal vessel; *gl.* œsophageal glands; *int.* beginning of intestine; *ne. co.* nerve-cord; *neph.* nephridia; *œs.* œsophagus; *palp.* palp; *para.* parapodia; *perist.* peristome; *perist. tent.* peristomial tentacles; *ph.* pharynx with its jaws; *præst.* prostomium; *tent.* prostomial tentacles; *vent. vess.* ventral vessel.

The **wall of the body** consists of a cuticle, an epidermis or deric epithelium, muscular layers, and the parietal layer of the cœlomic epithelium (*par. peri.*). The cuticle (*cut.*) is a thin chitinous layer which exhibits an iridescent lustre due to the presence of two intersecting systems of fine lines; it is perforated by numerous minute openings, the openings of the epidermal glands. The epidermis (*ep.*) is very thin, except on the ventral surface, where it becomes considerably thickened. It consists of a layer of cells containing numerous twisted unicellular glands, which are most abundant on the ventral surface, particularly near the bases of the parapodia; on the dorsal surface the epidermis contains plexuses of fine blood-vessels. The muscular layers are two in number—an external in which the fibres run circularly (*circ. mus.*), and an internal, in which they run longitudinally. The latter is not a continuous layer, but consists of four bundles of fibres, two dorso-lateral (*dors. long. mus.*) and two ventro-lateral (*vent. long. mus.*).

Nereis has a well-developed system of **vessels** filled with blood of a bright red colour. A main *dorsal vessel* (Figs. 281 and 282, *dors. vess.*) runs from one end of the body to the other above the alimentary canal, and is visible in places through the body-wall in the living animal. It, as well as the majority of the vessels, undergoes contractions which are of a *peristaltic* character—waves of contraction passing along the wall of the vessel so as to cause the movement of the contained blood. These peristaltic contractions are more powerful in the case of the dorsal vessel than in that of any of the others, and run with

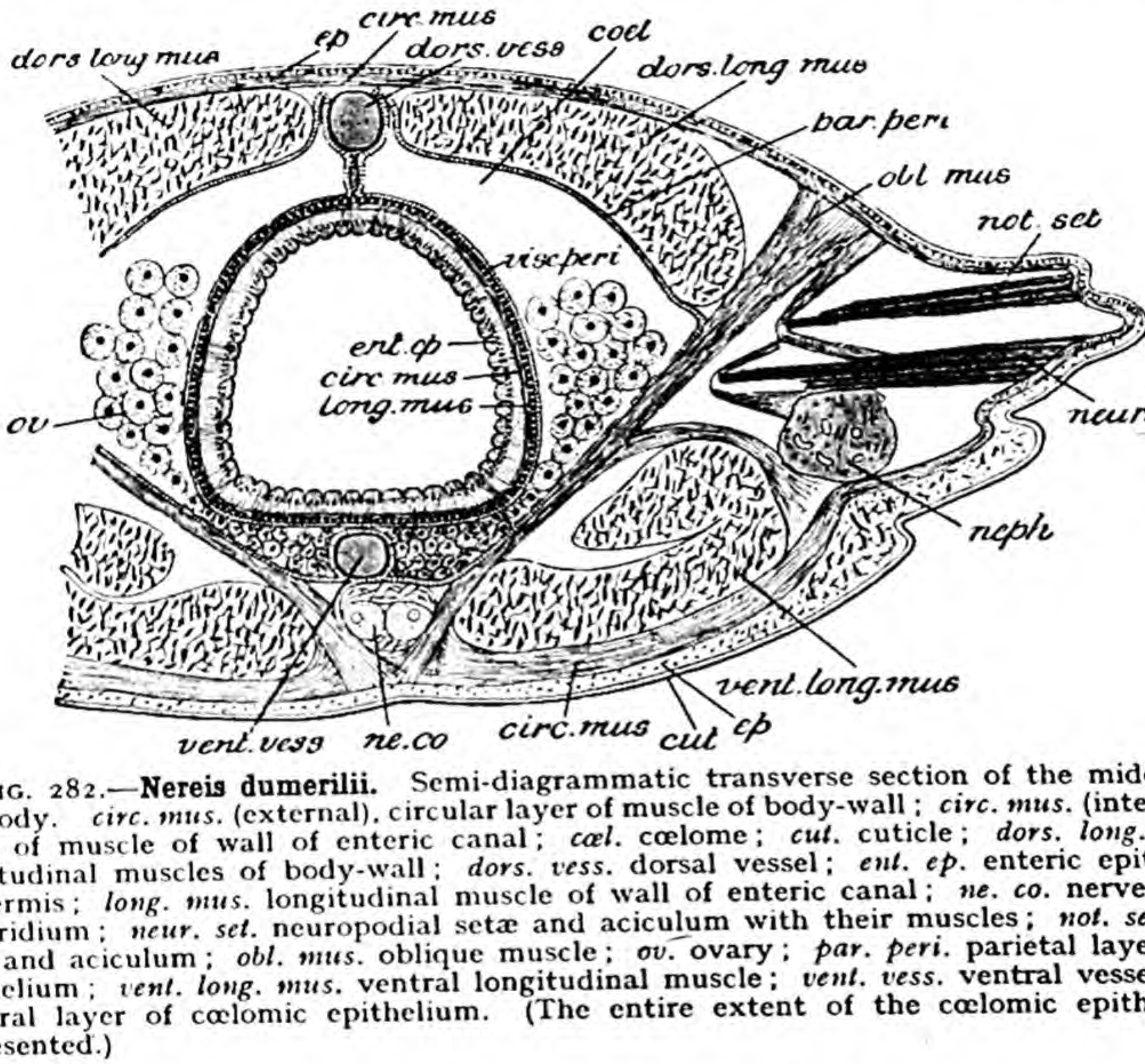


FIG. 282.—**Nereis dumerilii.** Semi-diagrammatic transverse section of the middle region of the body. *circ. mus.* (external), circular layer of muscle of body-wall; *circ. mus.* (internal) circular layer of muscle of wall of enteric canal; *cœl.* cœlome; *cut.* cuticle; *dors. long. mus.* dorsal longitudinal muscles of body-wall; *dors. vess.* dorsal vessel; *ent. ep.* enteric epithelium; *ep.* epidermis; *long. mus.* longitudinal muscle of wall of enteric canal; *ne. co.* nerve-cord; *neph.* nephridium; *neur. set.* neuropodial setæ and aciculum with their muscles; *not. set.* notopodial setæ and aciculum; *obl. mus.* oblique muscle; *ov.* ovary; *par. peri.* parietal layer of cœlomic epithelium; *vent. long. mus.* ventral longitudinal muscle; *vent. vess.* ventral vessel; *visc. peri.* visceral layer of cœlomic epithelium. (The entire extent of the cœlomic epithelium is not represented.)

great regularity from behind forwards, so as to drive a current of blood in that direction. The contractions are brought about partly by a series of muscular fibres which are arranged in rings round the wall of the vessel at short intervals; but the wall of the vessel is itself contractile.

Along the middle of the ventral surface below the alimentary canal runs another large longitudinal vessel, the *ventral vessel* (*vent. vess.*), in which the current of blood takes a direction from before backwards. Connecting the dorsal and ventral vessels, there are in each segment two pairs of loop-like transverse vessels which give off branches to the parapodia, the

alimentary canal, and neighbouring parts. Some of these branches communicate with plexuses of fine vessels in the interior of the lobes of the parapodia and in the integument of the dorsal surface, and with dilatations or sinuses situated in the bases of the parapodia. A delicate longitudinal *neural* vessel accompanies the nerve-cord.

Nereis is devoid of any gills; but there can be little doubt that the lobes of the parapods with their rich blood-supply, and the areas of integument occupied by plexuses of blood-vessels, subserve the function of respiration.

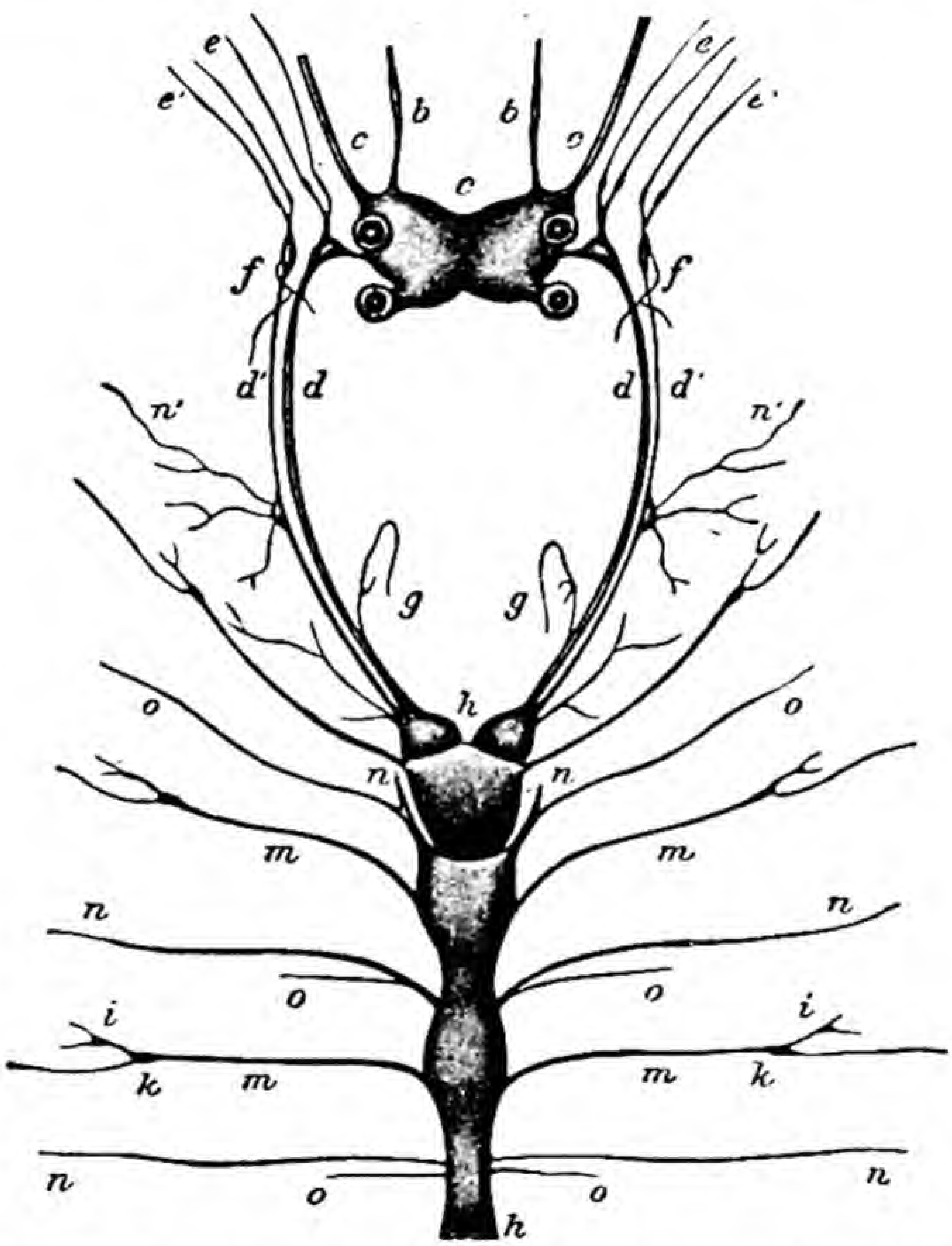


FIG. 283.—**Nereis.**—Anterior portion of nervous system, comprising the brain (*c*), the œsophageal connectives (*d*), and the anterior part of the ventral nerve-cord (*h*). (After Quatrefages.)

There is a well-developed **nervous system** (Fig. 283), which is bilateral and metameric in its arrangement, like the other systems of organs. Situated in the prostomium is a large bilobed mass of nerve-matter containing numerous nerve-cells, the *cerebral ganglion* or *brain* (*c*). This gives off *tentacular* nerves to the tentacles and palpi, and two pairs of short thick *optic* nerves to the eyes. Behind, two thick nerve-strands, the *œsophageal connectives* (*d*), curve round the mouth in the peristomium to meet on the ventral aspect behind the mouth and below the pharynx. The œsophageal connectives with the cerebral ganglion

thus form a ring around the anterior part of the enteric canal. From them are given off nerves to the two anterior pairs of peristomial tentacles. Running backwards from the point of union of the œsophageal connectives along the entire length of the body of the worm, on the ventral aspect, is a thick cord of nerve-matter, the *ventral nerve-cord* (*h*). In each segment this cord presents a little dilatation from which nerves are given off to the various parts of the segment; and each of these enlargements is really double, consisting of a pair of closely-united ganglia. The intermediate parts of the cord, between successive pairs of ganglia, are also double, consisting of a pair of longitudinal *connectives* enclosed in a common sheath. Given off behind from the cerebral ganglion is a system of fine nerves with occasional small ganglia, the *stomato-gastric* or *visceral system*, distributed to the anterior part of the alimentary

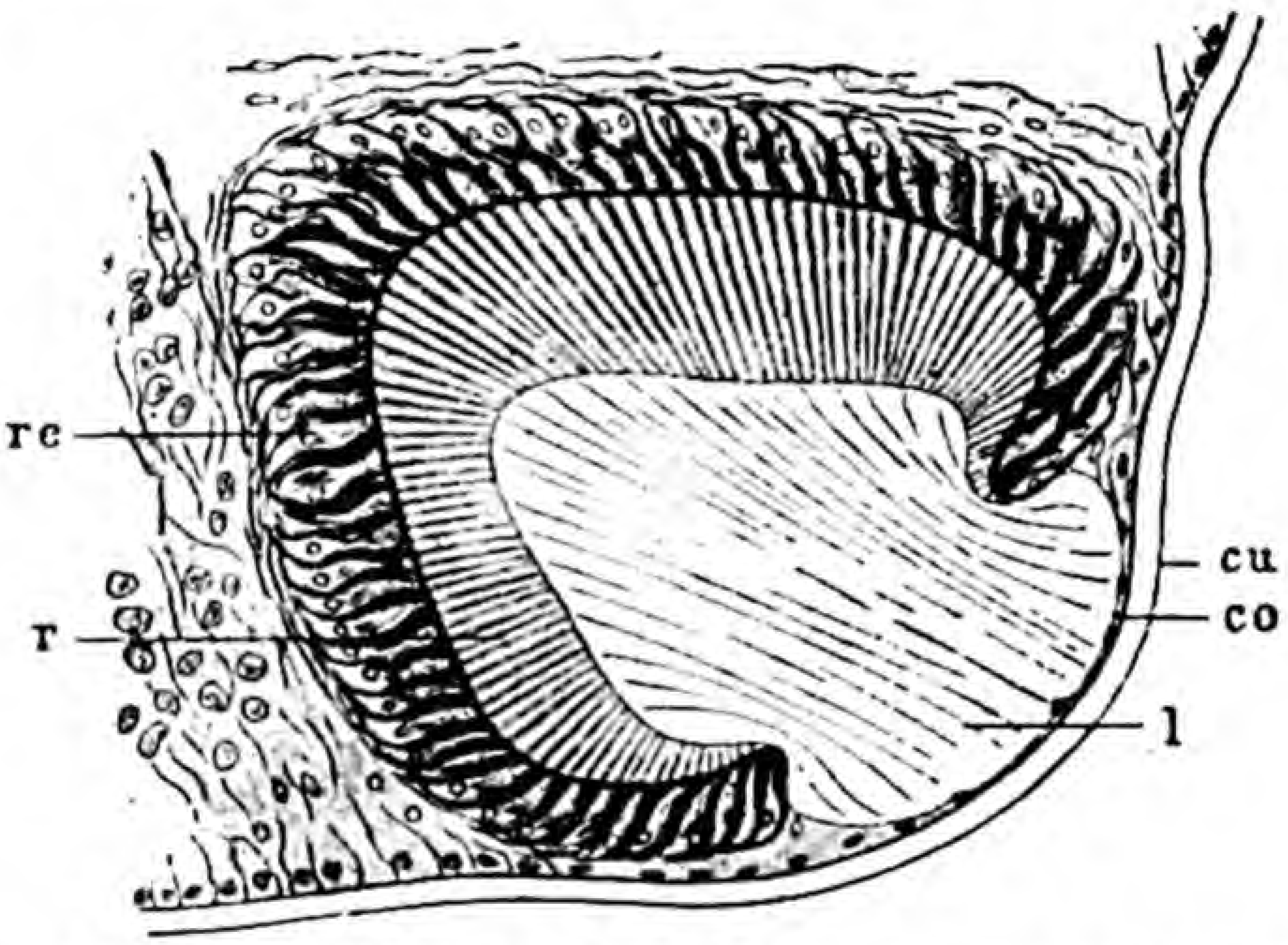


FIG. 284.—**Nereis.**—Section through one of the eyes. *co.* cornea; *cu.* cuticle; *l.* lens; *r.* layer of rods; *re.* retina. (After Andrews.)

canal. The first ganglion of the ventral cord, which is situated in the third segment, represents at least two double ganglia which have coalesced, as is shown by the fact that it gives off nerves to the two posterior pairs of peristomial tentacles and to the first pair of parapodia.

The tentacles and palpi, as well as the cirri, are probably organs of the sense of touch. The only other **sense-organs** are the four *eyes* and the two *nuchal organs*, all situated on the prostomium. The *eye* (Fig. 284) consists of a darkly pigmented cup, the *retina* (*re.*), with a small rounded aperture, the ***pupil***, and enclosing a mass of gelatinous matter, the *lens* (*l.*). The wall of the cup is composed of numerous long and narrow cells lying parallel with one another in a radial direction. The outer end of each cell narrows into a nerve-fibre forming part of the optic nerve; near this end is a nucleus; the main body of the cell is densely pigmented; the inner part projects towards the lens as a clear hyaline *rod* (*r.*). The cuticle of the general surface passes over the eye,

and a continuation of the epidermis, with its cells somewhat flattened, constitutes the *cornea* (*co*). The *nuchal organs* consist of a pair of pits lined by a special ciliated epithelium with gland-cells, situated in close contact with the posterior part of the brain near the posterior part of the prostomium on the dorsal side. They are regarded as olfactory in function.

The organs which perform the function of **excretion** are a series of metamerically arranged pairs of tubes, the *segmental organs* or *nephridia* (Figs. 281 and 282, *neph.*, Fig. 285) occurring in all segments of the body with the exception of several at the anterior and posterior ends. The nephridium consists of two parts—a body and a narrow anterior prolongation. The body is of an irregular oval shape directed nearly transversely, but slanting somewhat; the outer end, situated in the base of the parapodium near its middle, is much the narrower; the inner end is continuous with a narrow prolongation about equal in length to the body, which runs forwards and inwards to become attached to the mesentery. The external opening or *nephridiopore* (*ext. op.*) is a fine circular pore capable of being widened or contracted, situated on the ventral surface not far from the base of the ventral cirrus. It leads into a canal, ciliated except in its most external part, which runs through the anterior prolongation to its extremity, where it bends sharply back again and runs to the body, through which it pursues an extremely tortuous course to the outer end, and then bends back again and runs in the anterior prolongation to the extremity of the latter, where it opens into the cœlome through a ciliated bell or funnel (*fun.*), the *nephrostome*, projecting through the septum into the cavity of the segment next in front of that in which the body of the organ lies. The edge of the nephrostome is produced into a number of narrow ciliated processes not represented in the figure. Throughout its course the canal is excavated in a mass of nucleated material of a granular character not distinguishable into cells.

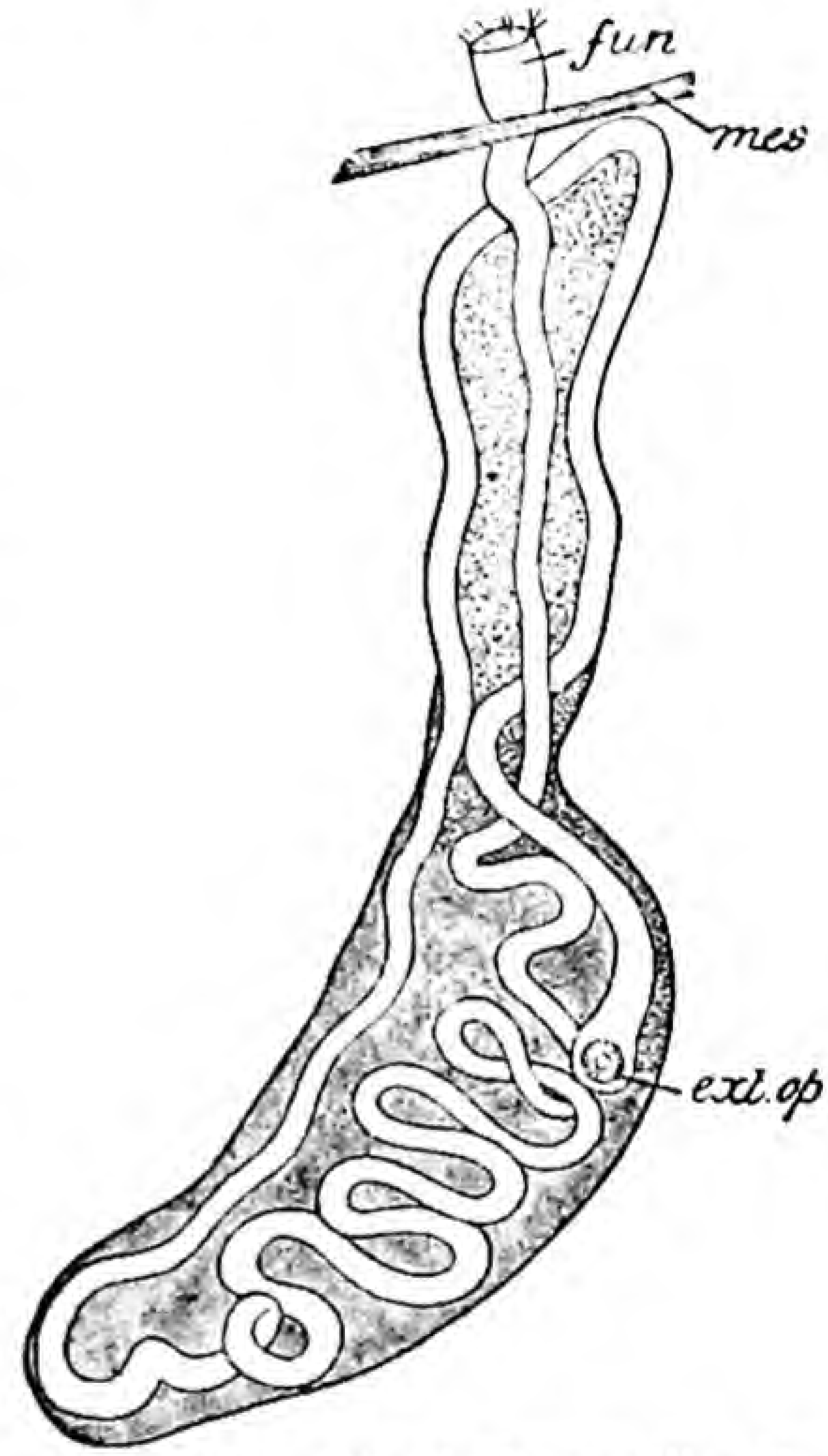


Fig. 285.—**Nereis dumerilii.** One of the nephridia. *ext. op.* external opening or nephridiopore; *fun.* internal funnel or nephrostome opening into the cœlome; *mes.* transverse mesentery or septum.

On the dorsal side of each segment, in close relation to the longitudinal muscular bundle, is a specially developed ciliated tract of the cœlomic epithelium of the nature of a short funnel without external aperture, the *dorsal*

ciliated organ. It has been assumed that at the time of sexual maturity an aperture is formed through the body-wall opposite this funnel, and that thus a genital duct of a temporary character becomes formed; but no such opening has ever been observed.

Nereis is unisexual. The **sexual elements**, ova or sperms, are formed from temporary masses of cells, *ovaries* or *testes*, which are developed towards the breeding season by a proliferation of the cells of the membrane (cœlomic epithelium) lining the cœlome and the structures it contains. In *Nereis dumerilii* there is in the male only a single pair of these proliferating masses of cells (*testes*), situated in one of the segments between the nineteenth and the twenty-fifth. But in other species of Nereis they are much more numerous. These, during the season of their active development, give off groups of cells which become disseminated throughout the cœlomic fluid. The original cells (mother-cells) undergo division into smaller cells, each of which develops into a sperm with a minute rod-shaped *head* and a long vibratile flagellum or *tail*. In the female the *ovaries* (Fig. 282, *ov*.), formed by a similar process of proliferation, take the form of rounded masses of cells, metamerically arranged, surrounding the principal vessels throughout the length of the body. The young ova become detached from the ovaries, and attain their full development while floating about in the cœlomic fluid. Both ovaries and testes dwindle after they have given off the sexual cells, and at the non-breeding season of the year are not to be detected.

Ova and sperms, when fully ripe, are discharged, reaching the exterior probably through apertures temporarily formed by rupture of the body-wall, and fertilization takes place by contact between the two sets of elements while floating freely in the sea-water.

Nereis dumerilii is an extremely *variable* species. If we compare a number of specimens, we find numerous **individual differences** between them. The most striking of these are differences of colour and of the number of segments in the body; but a careful examination reveals many other points in which individuals differ. Thus the precise form of the lobes of the parapodia, together with the number of setæ in the two bundles, varies; so also do the relative length of the tentacles, the number of teeth on the jaws, and the number and arrangement of the denticles in the buccal cavity. Not only are such individual differences common, but the species occurs in two distinct forms or *phases*, which differ from one another so widely that they have been referred to distinct genera. One of these is the *Nereis* phase, which is that described in the preceding paragraphs. A Nereis dumerilii may become sexually mature in this form, or may first undergo a series of changes by which it becomes converted into the second or *Heteronereis* phase (Fig. 277, *B*). The principal changes which take place during this metamorphosis are a great increase in the size of the eyes, and a marked modification of the parapodia

in the posterior portion of the body, the lobes becoming larger and more leaf-like, and the setæ of the Nereis being superseded by others which are considerably longer, more numerous, and somewhat oar-shaped. The Heteronereis, instead of creeping about on the bottom, swims about actively through the water by wriggling movements of the body combined with active paddling movements of the parapodia with their long setæ. After a time the Heteronereis, like the Nereis, becomes sexually mature, developing ova and sperms, the latter of which differ remarkably in shape from those of the Nereis phase.

Development.—The egg of Nereis when first discharged is enclosed in a

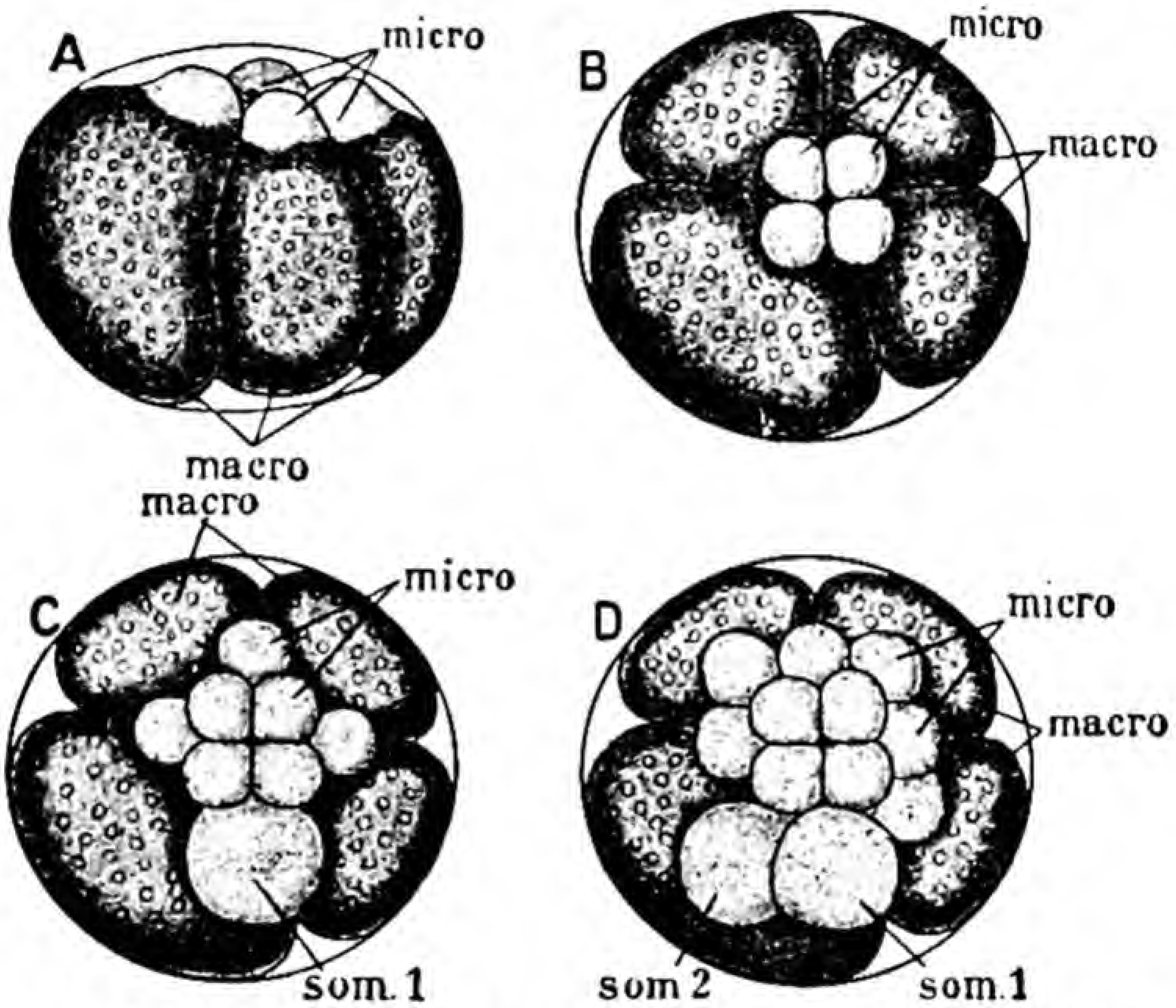


FIG. 286.—**Nereis.** Early stages in the development. *A*, lateral view of eight-celled stage; *B*, the same from above; *C*, stage of the formation of the first somatoblast; *D*, stage at which both somatoblasts are present; *macro.* macromeres; *micro.* micromeres; *som.* 1, *som.* 2, first and second somatoblasts. (After Westinghausen.)

transparent thick gelatinous envelope, within which are two membranes—an outer, very thin and delicate, and an inner (*zona radiata*), thicker and very distinctly striated in a radial direction. The protoplasm of the ovum contains a number of oil-drops and yolk-spherules. When fertilization takes place the yolk-spherules move away from what is destined to become the upper pole of the egg, leaving a polar area composed of granular protoplasm. The zona radiata disappears, and the contents of the ovum undergo for a time amœboid changes of form. Then the spherical form is reassumed, two small bodies—the *polar bodies*—are thrown off at the upper pole, and the process of cleavage begins (Fig. 286). This is of the spiral type, and up to a fairly advanced stage corresponds very closely with the cleavage of the Polyclad egg as described on

page 253. The zygote divides first into two parts, then into four. One of these (A, B) is larger than the rest. From these four cells—the macromeres—there are separated off in succession three sets or quartettes of *micromeres*, making twelve in all. One of these, belonging to the second set, somewhat larger than the others and differing from them in its subsequent history, is termed the *first somatoblast* (C, D, *som.* 1); a *second somatoblast* (*som.* 2) is soon given off in the fourth quartette from the same macromere that gave origin to the first.

The germinal layers are now all established. The micromeres constitute the *ectoderm*, destined to give rise to the epidermis and all its derivatives, to the cerebral ganglion and nerve-cord, to the œsophagus and rectum. The macromeres eventually give origin to the cells of the *endoderm*, forming the internal epithelium of the alimentary canal. The second somatoblast gives rise to the entire *mesoderm* of the Annelid and contributes a few small cells to the endoderm of the intestine. As the micromeres multiply by division, they form at first a cap of small cells over the upper pole of the embryo; eventually the cap extends so as completely to cover the four macromeres and the descendants of the somatoblasts, except at one point, the *blastopore*, at the lower pole, where the investment remains for a time incomplete. When the blastopore closes, the process of epibolic gastrulation is completed. A thickening of the layer of ectoderm cells, the *apical plate*, in the middle of what is destined to form the head-end of the embryo, is the rudiment of the cerebral ganglion: in close relation to it are formed a pair of pigment-spots, the larval eyes. From the middle of the head-end projects a tuft of cilia (Fig. 287, *A*, *ap. cil.*). Encircling the body of the larva behind this is a thickened ridge, the *prototroch* (*prot.*), the cells of which develop strong cilia. Just behind the prototroch the cells of the ectoderm become pushed inwards in the middle of what will eventually become the ventral surface, so as to line a sort of depression or pouch; this is the *stomodæum* (*st.*) or rudiment of the mouth and œsophagus. The anus (*an.*) does not appear until later; the position which it will subsequently occupy is indicated at this stage by a pigmented area (*pig. ar.*) marking the point at which the blastopore becomes closed. The first and second somatoblasts divide to form a mass of small cells which extend on the ventral surface behind the prototroch and mouth, constituting what is termed the *ventral plate*; of this plate the more superficial cells are descendants of the first somatoblast; and those situated more deeply are derived from the second somatoblast. A superficial thickening of the ectoderm along the middle of the ventral plate is the rudiment of the ventral nerve-cord (*neur. pl.*); the deeper cells divide and extend to form a pair of *mesoderm-bands* or *muscle-plates*, from which the muscles of the body-wall are developed; the muscular layers of the wall of the alimentary canal are derived from certain of the same set of cells which migrate inwards from the lower end.

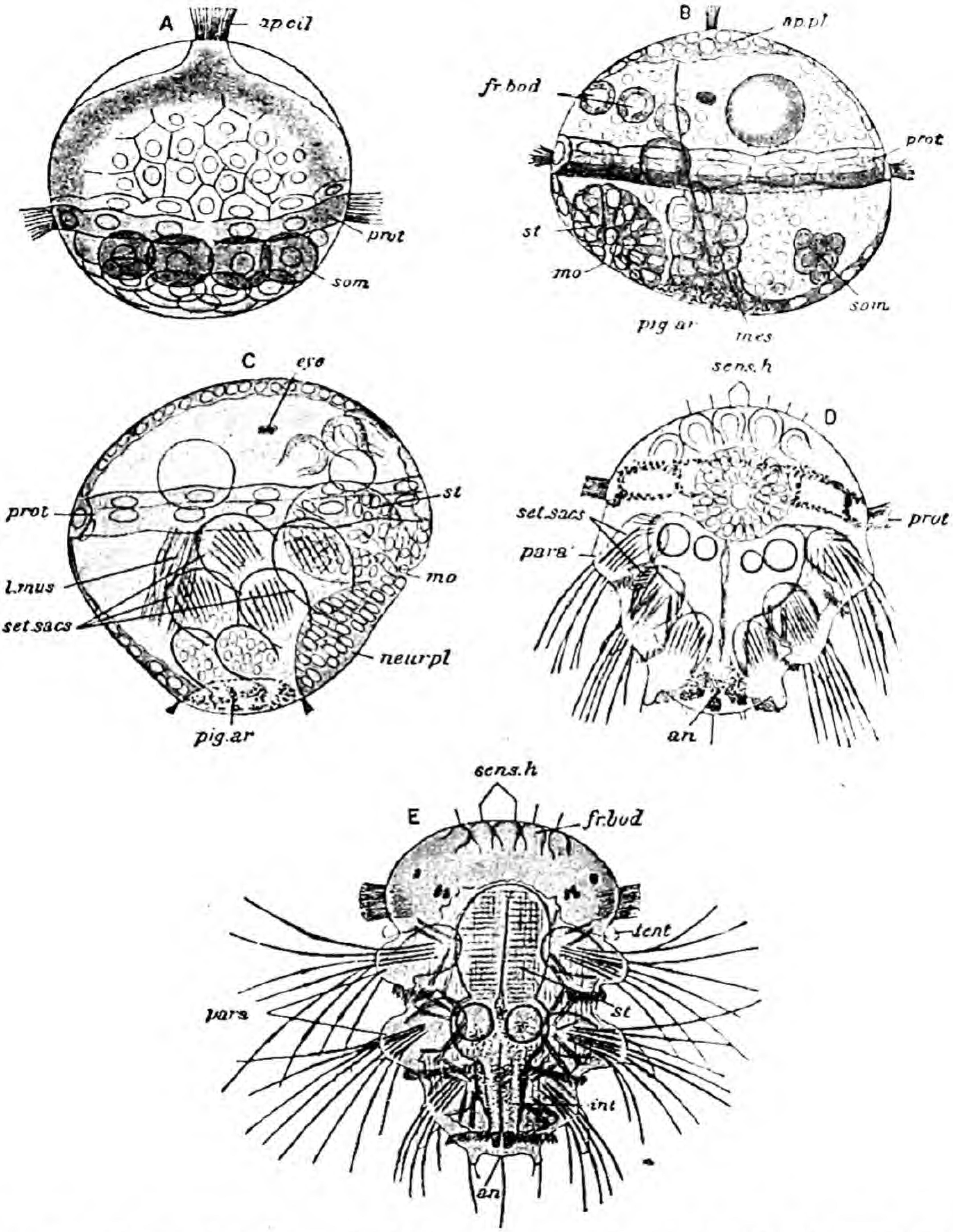


FIG. 287.—**Nereis.** Later stages in the development. *A*, stage at which the prototroch and the apical tuft of cilia first become distinct. *B*, somewhat later stage, in which the stomodæal invagination is being formed, and the rudiments of the mesoderm bands are distinct; *C*, late trochophore stage, in which there are rudiments of the setigerous sacs; *D*, somewhat later stage, in which the parapodia have begun to become prominent and the provisional setæ project freely; *E*, larva with three segments. *an.* anus; *ap. cil.* apical cilia; *ap. pl.* apical plate; *eye.* eye; *fr. bod.* frontal bodies; *int.* intestine; *l. mus.* longitudinal muscle; *mes.* mesoderm; *mo.* mouth; *neur. pl.* neural plate; *para.* parapodia; *pig. ar.* pigmented area; *prot.* prototroch; *sens. h.* sensory hairs; *set. sacs.* setigerous sacs; *som.* second somatoblast and group of cells formed from it; *st.* stomodæum; *tent.* peristomial tentacles. (After E. B. Wilson.)

A pair of micromeres separated from the rest at an early stage are destined to form the larval excretory organs, or larval nephridia: at first situated at the upper end, they sink below the surface and migrate downwards till they come to lie below the prototroch; each then elongates, and a number of vacuoles which have become formed in the interior coalesce in such a way as to form a long, narrow canal. The embryo has now reached the completed trochophore stage.

The endoderm cells become arranged so as to bound a canal-like space, the beginning of the lumen of the middle part of the alimentary canal (œsophagus and intestine, *int.*), the cells subsequently giving rise to the enteric epithelium. This canal becomes continuous in front with the stomodæum, and behind with a second smaller ectodermal invagination, the *proctodæum*, which arises in the position of the former pigment-area. The part of the larva behind the prototroch now elongates, and two pairs of invaginations, the *setigerous sacs* (*set. sacs*), appear at its sides: in the interior of these, to which a third pair is soon added, are developed setæ which grow out to a great relative length as the *larval* or *provisional setæ*. Constrictions soon appear marking off the first three segments, and at the same time the mesoderm bands undergo a corresponding division into three pairs of mesoderm segments. The mesoderm segments of each pair grow inwards towards one another and surround the alimentary canal: in the interior of each appears a cavity which is the beginning of a segment or chamber of the cœlome. As the two mesoderm segments become closely applied to one another and unite around the alimentary canal, their two cavities also come into close relation, and eventually are separated from one another only by thin vertical septa, forming dorsal and ventral mesenteries which subsequently disappear. Successive mesoderm segments also come into close relationship with one another, their cavities eventually only remaining separated by thin transverse partitions, which form the intersegmental septa.

The region in front of the prototroch becomes modified to form the prostomium of the adult. The part immediately behind forms the peristomium, which bears setæ, and is to be looked upon as the specially modified first segment. The body increases in length, and additional segments with their setigerous sacs become distinguishable (*E*), until, on the development of the tentacles, the outgrowth of the parapodia (*para.*) with their cirri and the permanent setæ (which replace those first formed), the formation of the full number of segments, and the completion of the internal organs, the adult condition of the worm is attained.

b. The Earthworm (*Lumbricus*).

General External Features.—The Earthworm (Fig. 288) has a long narrow body, which may be described as approximately cylindrical, but slightly depressed towards the posterior end. Dorsal and ventral surfaces are readily

recognizable, the latter being much paler in colour than the former, and exhibiting a slight flattening; the anterior end is distinguishable in the living animal as that which is directed forwards in the ordinary creeping movements of the worm. The surface, as in the case of Nereis, is very distinctly marked out into segments or metameres by a series of ring-like constrictions; the segments, which are very numerous, amounting to about 150, are somewhat longer towards the anterior end than they are farther back.

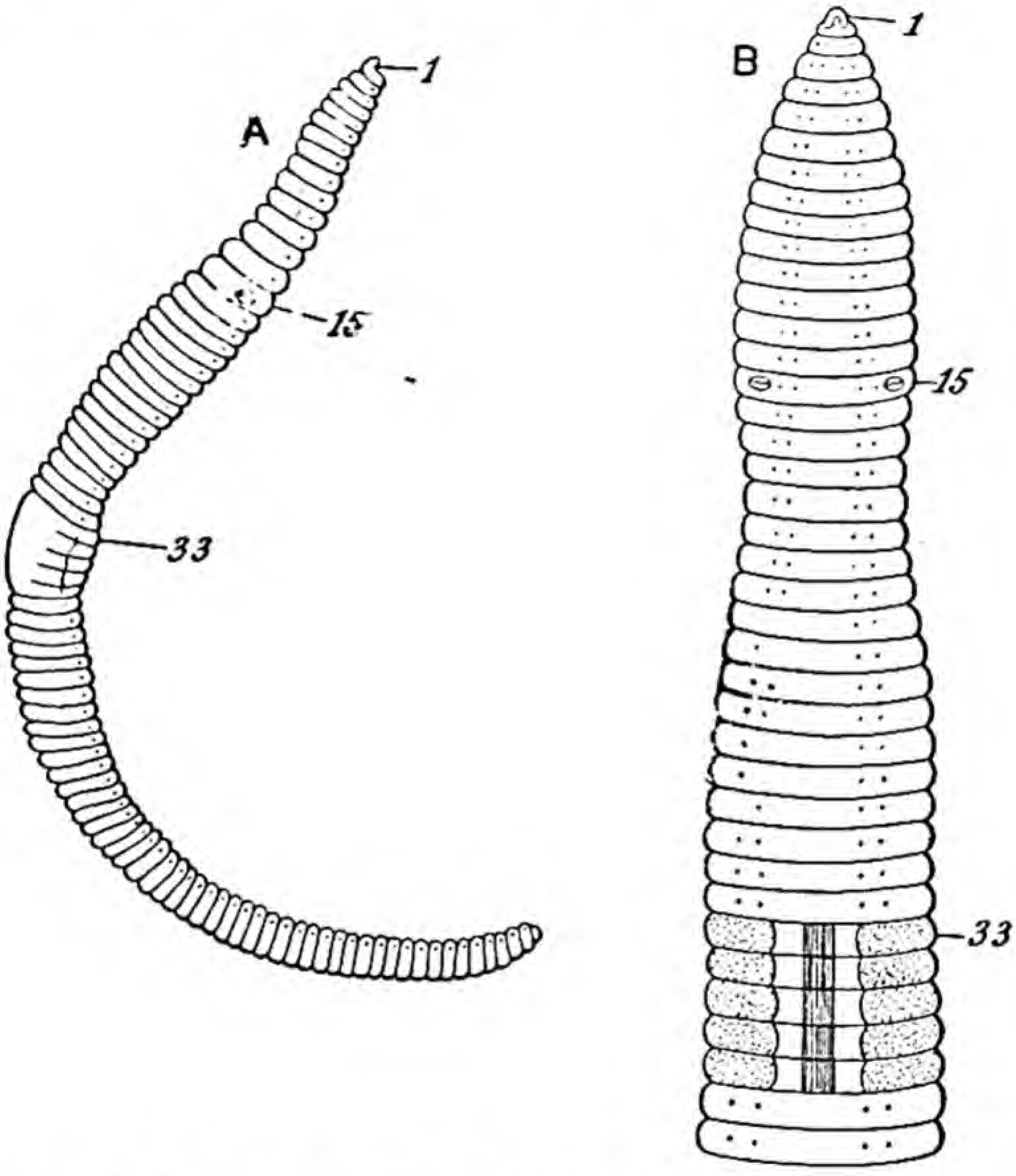


FIG. 288.—**Lumbricus.** *A*, entire specimen, lateral view; *B*, ventral view of anterior portion of the body, magnified. *1*, prostomium; *15*, *33*, fifteenth and thirty-third segments. Each of the black dots represents a pair of setæ. (After Vogt and Jung.)

At the extreme anterior end is a rounded lobe, the *prostomium*, immediately behind and below which is the opening of the mouth. Next to the prostomium is the most anterior segment, the *peristomium*, which bounds the mouth behind. The eyes and tentacles present in Nereis are not represented. On the most posterior segment, the *anal segment*, is a small median opening, the *anal aperture*. A limited region of the body in front of the middle, comprising five or six segments, has a swollen appearance: this is termed the *clitellum*. There are no parapodia like those of Nereis, but running along the lower surface of

the worm are to be recognized with the aid of a lens four double rows of short bristles or setæ (Fig. 289), a pair of each row occurring in each segment, which thus possesses eight altogether. The extremities of all these setæ are directed backwards, and they act as fulcra for the forward movements of the worm on the surface of the ground or in the interior of its burrow. The setæ in the clitellum, and those in the neighbourhood of the genital apertures, are much slenderer than the rest. Along the middle line of the dorsal surface, from about the eleventh segment backwards, is a row of small apertures, one at the line of division between each contiguous pair of segments: these, which are termed the *dorsal pores*, perforate the body-wall and open internally into the cœlome. Through these cœlomic fluid is capable of being discharged, covering the surface with a thin layer which may protect the worm from desiccation or from contact with irritating substances. On the ventral surface are two rows of minute apertures—a pair on each segment—the *excretory apertures* or *nephridiopores*. On the ventral surface of the fifteenth segment (Fig. 288, *15*) is a pair of slit-like apertures with somewhat tumid lips, the *male reproductive apertures*; and on the segment immediately in front—the fourteenth—are two smaller rounded apertures, the *female reproductive apertures*. In the intervals between the ninth and tenth and tenth and eleventh segments are two pairs of small pores, the openings of the *receptacula seminis*.

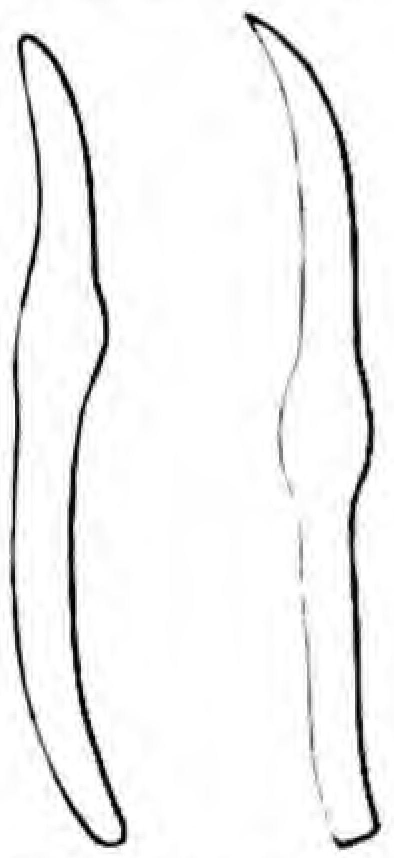


FIG. 289.—**Lumbricus.** Setæ, highly magnified.

The **body-wall** (Fig. 290) consists of a *cuticle*, an *epidermis* or *deric epithelium*, a *dermis*, *muscular layers* with associated connective tissue, and, lining the inner surface, a thin cellular membrane, the *peritoneum* or *cœlomic epithelium*. The *cuticle* (*cut.*) is similar to that of Nereis, and has a similar iridescent lustre; it is perforated by numerous minute apertures. The epidermis consists, except on the clitellum, of a single layer of cells elongated in the vertical direction: many of these cells have the character of unicellular glands; many others are sensory cells, and are connected by fine nerve-fibres with the nerve-cord. On the clitellum the epidermis is thickened, and blood-vessels extend between the cells. Below the epidermis is a layer of connective tissue, the *dermis*. The muscular fibres which make up the greater part of the thickness of the body-wall are arranged in two principal sets—a layer of circularly arranged fibres (*circ. mus.*) situated externally, immediately below the dermis, and a layer of longitudinally arranged fibres (*long. mus.*) situated internally. The circular layer is interrupted at all the intervals between the segments; the longitudinal layer is interrupted along a series of longitudinal lines, so as to be divided into seven bundles.

The setæ (Fig. 289) are lodged in sacs, the *setigerous sacs* (see Fig. 300), lined by a continuation of the epidermis. In the region of the body in which

the reproductive organs are lodged some of these sacs are enlarged and glandular, and receive the special name of *capsulogenous glands*.

The **enteric canal** (Fig. 290) is, as in Nereis, a tube which runs through the entire length of the body from the mouth at the anterior to the anus at the posterior end. As in the case of Nereis, it lies in a cavity, the *cœlome*, lined by a thin cellular membrane, the *peritoneum* or *cœlomic epithelium*, and filled with a fluid, the *cœlomic fluid*, containing colourless corpuscles. The cœlome is divided into a series of chambers corresponding to the segments

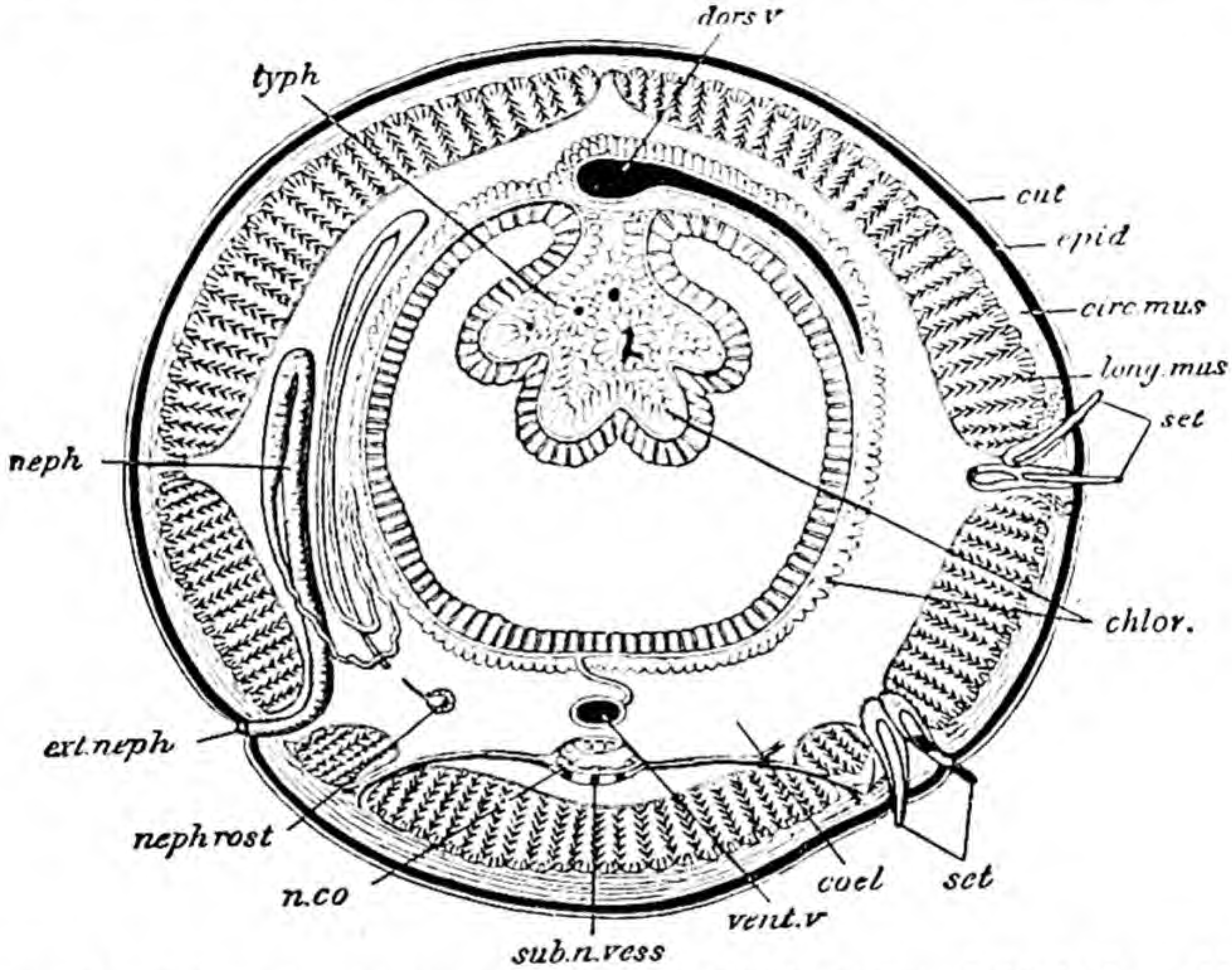


FIG. 290.—**Lumbricus,** transverse section of the middle region of the body. *chlor.* layer of chloragogenous cells; *circ. mus.* layer of circular muscular fibres; *cœl.* cœlome; *cut.* cuticle; *dors. v.* dorsal vessel; *epid.* epidermis; *ext. neph.* nephridiopore; *long. mus.* longitudinal muscle; *neph.* nephridium; *nephrost.* nephrostome; *n. co.* nerve-cord; *set.* setæ; *sub. n. vess.* sub-neural vessel; *typh.* typhlosole; *vent. v.* ventral vessel. (After Marshall and Hurst.)

by a series of delicate transverse partitions, the *septa* or *mesenteries*, consisting of folds of the peritoneal membrane enclosing muscular fibres.

The mouth leads into a small *buccal cavity*. This is followed by a much larger, thick-walled, rounded chamber, the *pharynx* (*ph.*). From the wall of the pharynx there run outwards to the body-wall a number of radially arranged bundles of muscular fibres which, when they contract, draw the pharynx backwards, and at the same time dilate it. Behind the pharynx follows a comparatively narrow tube, the *œsophagus* (*œs.*), which extends through about seven segments. At the sides of the œsophagus, in each of the segments ten, eleven, and twelve, is a pair of rounded projections. The first pair—the

œsophageal pouches—are hollow, and their cavities are in communication with the lumen of the œsophagus (*œs. gl.*). The other two pairs—the *calciferous glands*—are thickenings of the wall of the œsophagus, the fluid in the interior of which is milky, owing to its containing numerous particles of carbonate of lime; the numerous small cavities which they contain are in communication with the œsophageal pouches. Posteriorly the œsophagus is continuous with a rounded thin-walled chamber, the *crop* (*cr.*), and this is followed by a very thick-walled chamber, also of rounded form, the *gizzard* (*giz.*). From this the intestine (*int.*) extends throughout the rest of the length of the body to the anal aperture. It is wide, with thick but soft walls, constricted opposite the septa, *i.e.* in the intervals between the segments. Running along the middle of its dorsal surface is a longitudinal fold, the *typhlosole* (Fig. 290, *typh.*), pro-

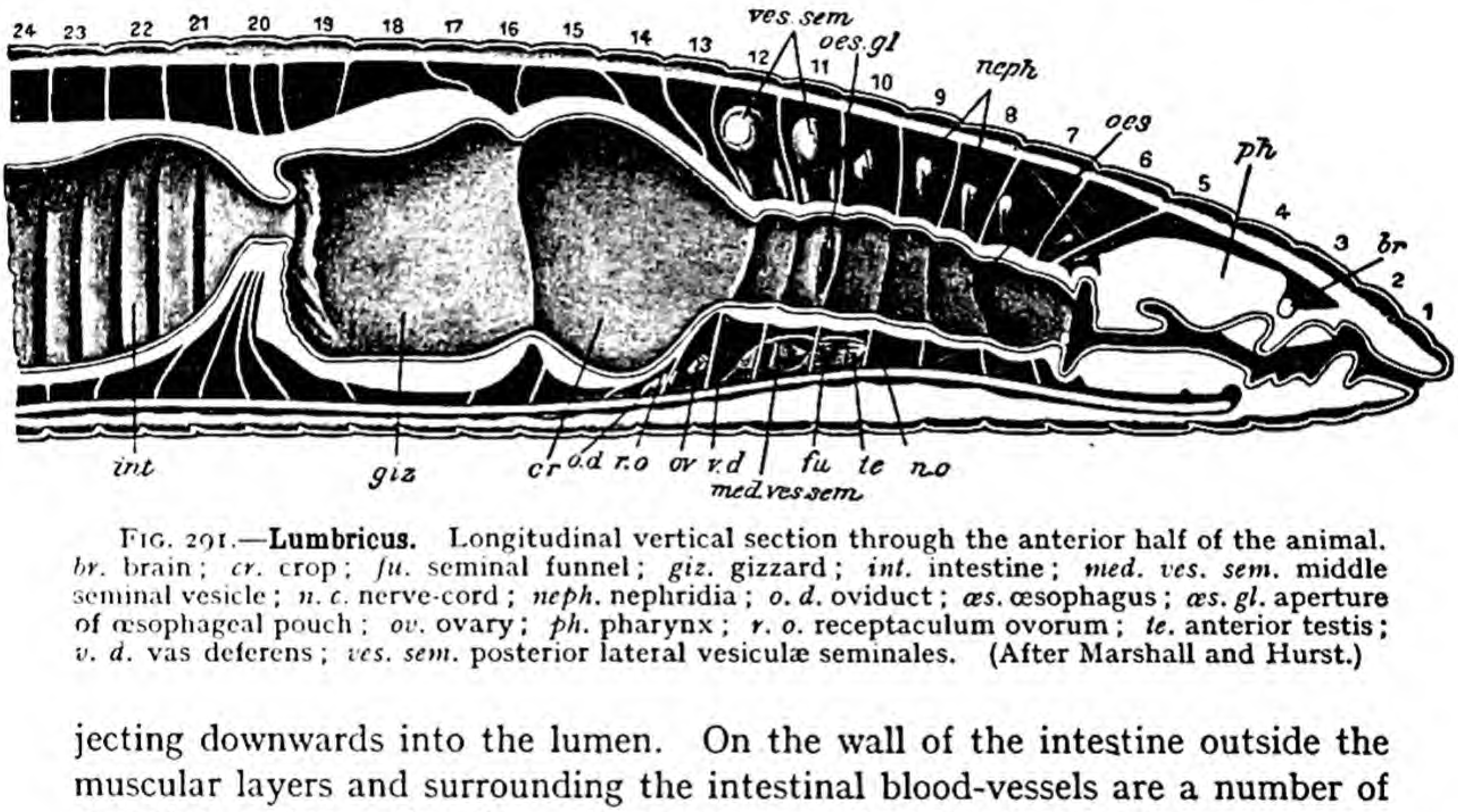


FIG. 291.—**Lumbricus.** Longitudinal vertical section through the anterior half of the animal. *br.* brain; *cr.* crop; *fu.* seminal funnel; *giz.* gizzard; *int.* intestine; *med. ves. sem.* middle seminal vesicle; *n. c.* nerve-cord; *neph.* nephridia; *o. d.* oviduct; *œs.* œsophagus; *œs. gl.* aperture of œsophageal pouch; *ov.* ovary; *ph.* pharynx; *r. o.* receptaculum ovorum; *te.* anterior testis; *v. d.* vas deferens; *ves. sem.* posterior lateral vesiculæ seminales. (After Marshall and Hurst.)

jecting downwards into the lumen. On the wall of the intestine outside the muscular layers and surrounding the intestinal blood-vessels are a number of granular, yellow cells—the *chloragogenous cells* (*chlor.*): these are specially abundant in the typhlosole. The terminal part, situated in the last segment, is termed the *rectum*.

The whole alimentary canal is lined internally by a cuticle, which is thicker in the gizzard than elsewhere, and by a single layer of ciliated columnar epithelial cells, the *enteric epithelium*. Some of these cells, more granular than the others, grouped in certain regions—more particularly along the typhlosole—are of the nature of unicellular digestive glands, secreting a digestive fluid. Others seem to be specially concerned in the absorption of the digested food. External to this is a layer of connective tissue, between which and the external covering of yellow cells are muscular fibres, of which there are two layers, an

external longitudinal and an internal circular. These layers are greatly thickened in the walls of the pharynx and of the gizzard.

The Earthworm, like Nereis, has a well-developed **vascular system** consisting of blood-vessels with well-defined walls. The blood is bright red, the colour being due to the same colouring matter, viz. *hæmoglobin*, as in the case of the blood of the higher animals, occurring, however, not in corpuscles, but in the liquid part or *plasma*; corpuscles are present, but they are colourless. The main trunks are the *dorsal*, the *ventral*, the *sub-neural*, the two *lateral neural*, and a series of *transverse branches*. The *dorsal vessel* (Fig. 290, *dors. v.*) runs along the middle of the dorsal surface between the body-wall and the intestine; it is readily visible shining through the former in the living worm. The *ventral vessel* (*vent. v.*) lies below the alimentary canal, the *sub-neural* below this again under the nerve-cord; the *lateral neural* lie on either side of the nerve cord. The *transverse branches* correspond in number to the segments; they run round from the dorsal vessel to the ventral, giving off branches in their course. Five of them, viz. those in the seventh to the eleventh segments inclusively, are dilated and pulsate rhythmically; these have the function of driving the blood through the system of vessels, and are hence frequently termed the "hearts." The walls of the principal vessels are contractile, and assist in bringing about the movement of the blood, which is propelled in such a way as to run forwards in the dorsal vessel and backwards in the ventral, its direction of movement being regulated by a number of valves in the "hearts," the dorsal vessel, and the chief vessels connected with it.

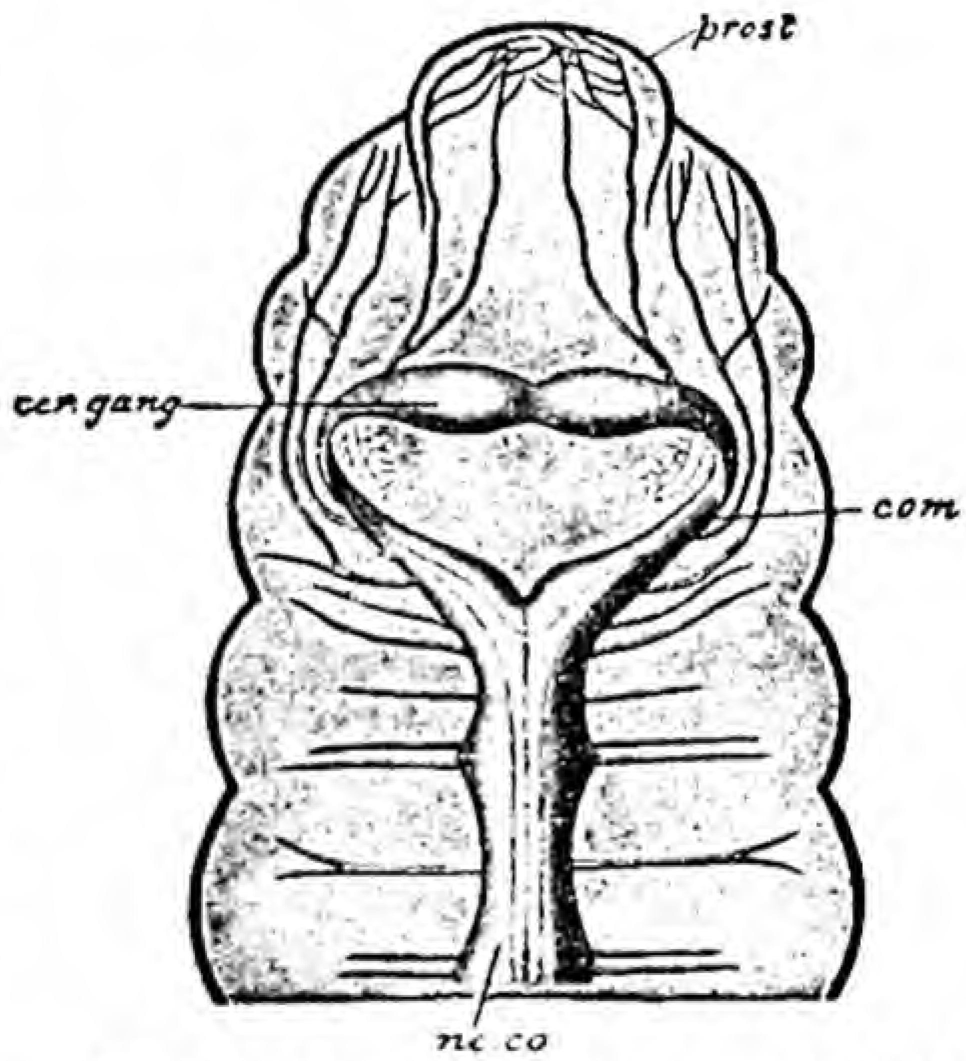


FIG. 292.—**Lumbricus.** Anterior portion of nervous system. *cer. gang.* cerebral ganglion or brain; *com.* œsophageal connectives; *ne. co.* ventral nerve-cord; *prost.* prostomium. (After Leuckart.)

The **nervous system** (Fig. 292) consists of a dorsal bilobed *brain* or *cerebral ganglion* and a double *ventral nerve-cord* together with a pair of *œsophageal connectives*, by which the former is connected with the anterior end of the latter. The *brain*, which is of small size, is situated in the third segment above the beginning of the alimentary canal; it is divided by a median constriction into two lateral parts of pyriform shape with their broad ends in contact. The connectives pass from this round the sides of the alimentary canal to unite in the middle below with the anterior end of the ventral nerve-cord. In this way a complete *nerve-ring* or *nerve-collar* surrounds the anterior part of the enteric canal in the third segment. From this the ventral nerve-

cord extends backwards to the posterior end of the body, and in each segment it presents a slight enlargement or ganglion, as it is usually termed, most conspicuous in the more posterior segments. The whole cord is double, consisting of two intimately united right and left parts. From the brain, nerves are given off to the prostomium; and from the ventral cord three pairs of nerves arise in each segment. From the œsophageal connectives a series of *stomatogastric* nerves pass to the pharynx and neighbouring parts of the alimentary canal.

The Earthworm is devoid of organs of sight or hearing. It exhibits sensitiveness to bright light, the sensitive elements being large cells of the epidermis devoid of pigment. The sense of hearing appears to be absent; but a faculty analogous to taste or smell, enabling the animal to distinguish between different kinds of food, is well developed. The *goblet-shaped bodies*, groups of narrow epidermal cells, most abundant on the prostomium and peristomium, have probably to do with this faculty.

The **organs of excretion**—the *segmental organs* or *nephridia* (Fig. 293)—are similar to those of Nereis, but somewhat more complicated. They are slender tubes which occur in pairs in all the segments of the body except the first three and the last. Externally each nephridium opens by one of the small nephridiopores, which have already been mentioned as occurring on the ventral surface; internally it ends in a funnel-shaped ciliated extremity with a crescentic slit-like aperture, the *nephrostome* (*nst.*), opening into the cavity of the segment in front of that in which the external aperture occurs. The tube is thrown into three loops attached to the posterior surface of the corresponding septum by a fold of membrane. Two parts are clearly recognizable—an inner narrow and an outer wide part: in the former the narrow central lumen is a perforation through the axis of a string of cells, and is thus *intracellular*: it is lined in parts with cilia arranged in two rows; in the latter (the *terminal vesicle*) the passage is lined by cells, and is thus *intercellular*, and there is a thick muscular investment. The nephridia are abundantly supplied with blood by means of nephridial branches of the ventral vessel.

Reproductive Organs.—The Earthworm is hermaphrodite. There are two pairs of very small flattened *testes* (Figs. 291, 294, *te, te'*), partly divided into a number of digitate lobes, situated in the tenth and eleventh segments. A pair of comparatively large sacs, the *anterior vesiculæ seminales* (*ant. ves. sem.*), lie partly in the cavity of the ninth segment, but extend into the tenth, where they coalesce in the middle to form a large median sac of somewhat irregular form, the *anterior sperm-reservoir* (*ant. sp. res.*). The anterior pair of testes project into this, and the cells destined to form the sperms, developed in the former, pass by dehiscence into the large median cavity. On either side is a large *ciliated funnel*, or *rosette* (*fun.*), leading outwards from the interior of the reservoir. A second pair of vesiculæ seminales (*mid. ves. sem.*), situated in the

eleventh segment, also open into the anterior sperm-reservoir. A third pair (*post. ves. sem.*), situated in the twelfth segment, unite in front to form the *posterior sperm-reservoir* (*post. sp. res.*), which lies in the middle of the cavity

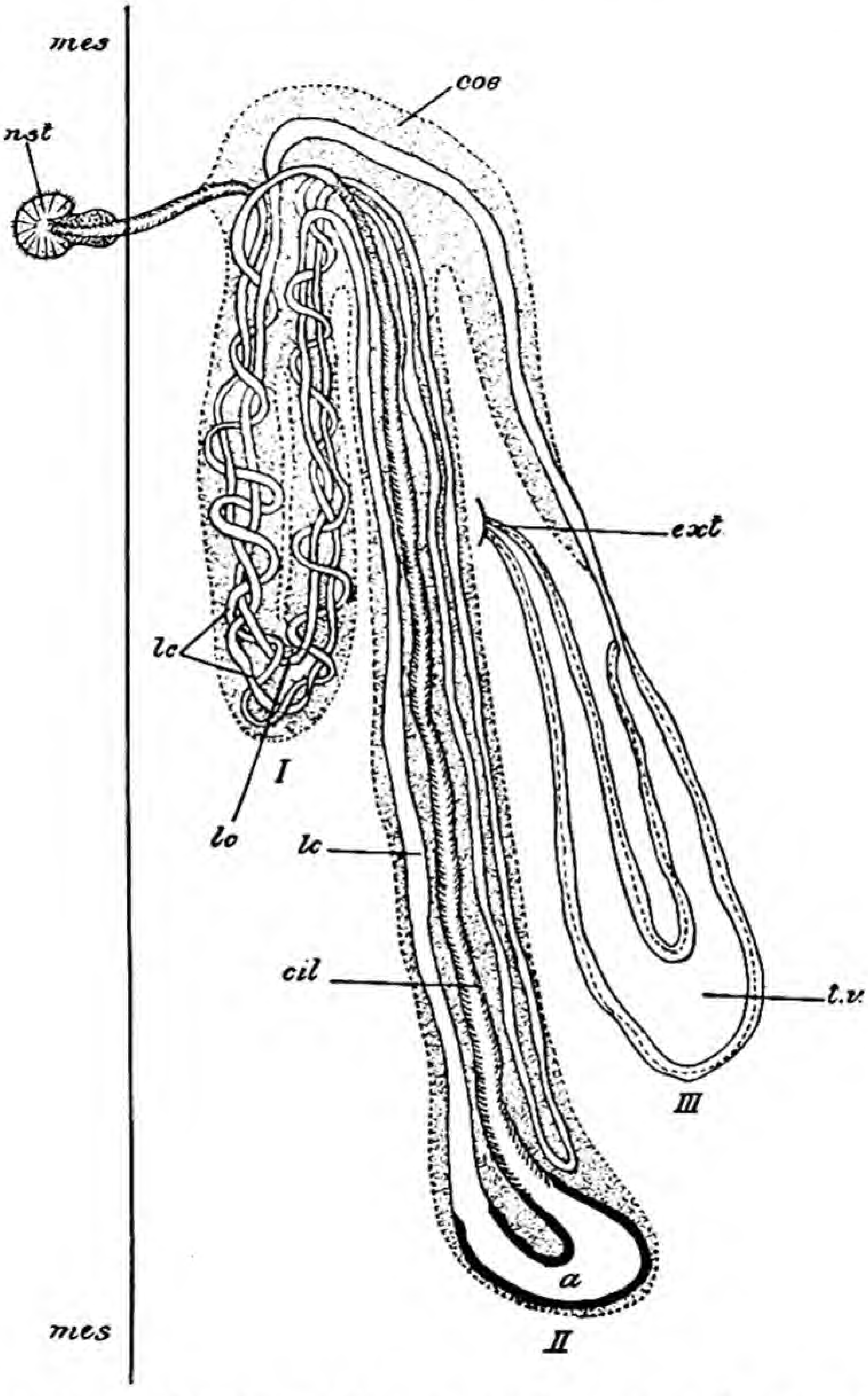


FIG. 293.—Nephridium of **Lumbricus** (diagrammatic).—*a.* ampulla between ciliated and non-ciliated parts of the intracellular canal; *cil.* ciliated part of the intracellular canal; *coe.* investment derived from the cœlomic epithelium; *ext.* nephridiopore; *lc.* non-ciliated part of the intracellular canal; *mes.* septum; *nst.* nephrostome; *t.v.* intercellular canal of the terminal vesicle. *I.—III.* the three principal loops. (From Meisenheimer, after Maziarski.)

of the eleventh segment. The posterior pair of testes have the same relation to this as the anterior pair have to the anterior reservoir; and a posterior pair of ciliated funnels (*fun.*) lead outwards from its cavity. Each ciliated funnel

passes into a narrow, somewhat convoluted duct, the *vas efferens*, and the two vasa efferentia of each side unite to form a *vas deferens* or *spermiduct* (*v. def.*), right or left as the case may be, which passes almost straight backwards to open by the corresponding male aperture on the fifteenth segment.

The female reproductive organs consist of a pair of *ovaries*, a pair of *oviducts* with a pair of *receptacula ovorum*, and two pairs of *receptacula seminis*. The *ovaries* (*ov.*) are minute pear-shaped bodies, which are situated in the thirteenth segment, attached to the septum between the twelfth and thirteenth. The

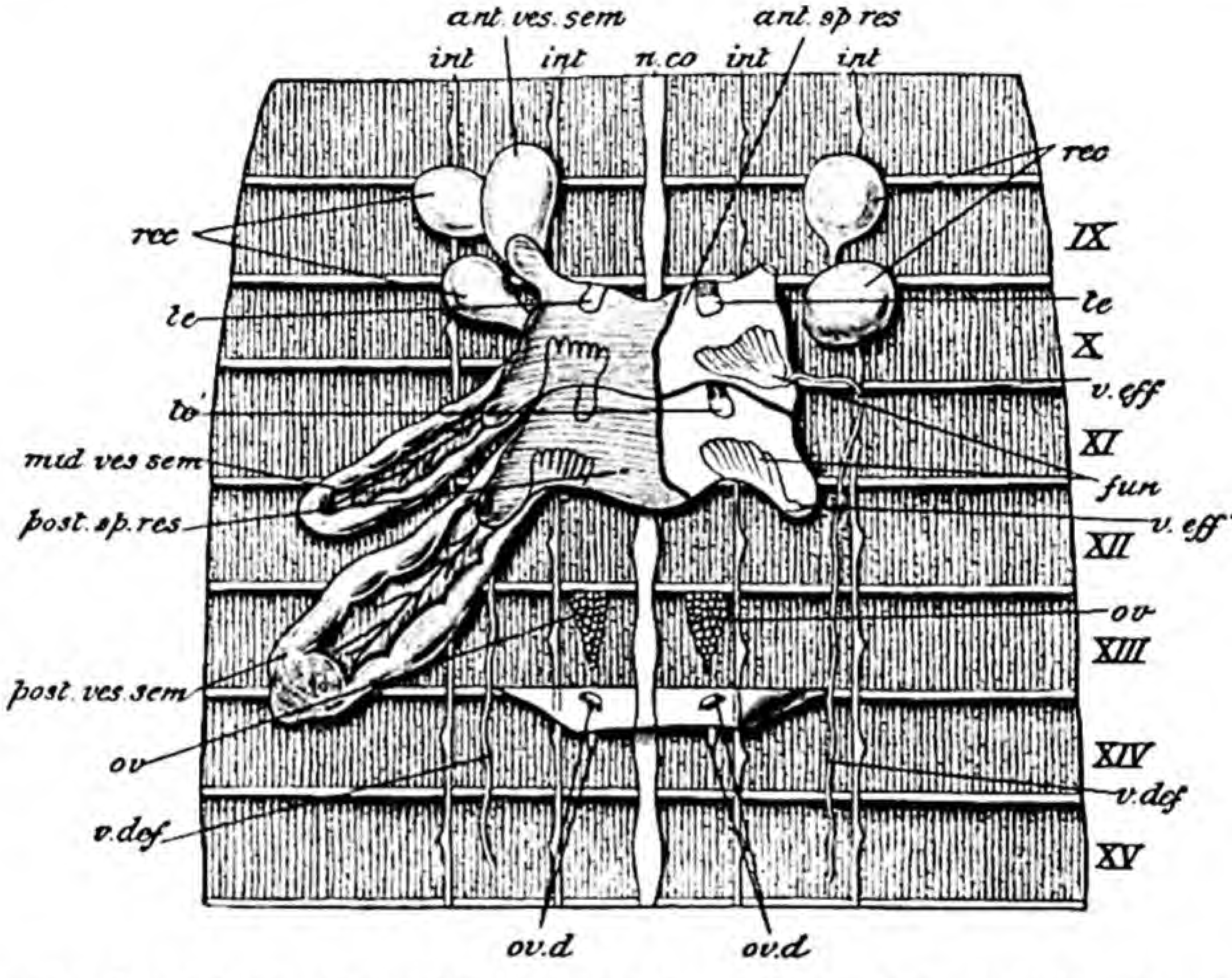


FIG. 294.—**Lumbricus.** Reproductive organs. *ant. sp. res.* anterior sperm reservoir; *ant. ves. sem.* anterior left vesicula seminalis; *fun.* funnel-like openings of vasa efferentia; *int.* intermuscular partitions; *mid. ves. sem.* middle vesicula seminalis; *n. co.* nerve-cord; *ov.* ovaries; *ov. d.* oviducts; *post. sp. res.* posterior sperm-reservoir; *post. ves. sem.* posterior vesicula seminalis; *rec.* receptacula seminis; *te*, anterior, and *te'*, posterior testes; *v. eff.* anterior, and *v. eff'.* posterior vas efferens; *v. def.* vasa deferentia. (After Vogt and Jung.)

oviducts (*ov. d.*) are a pair of short tubes, each with a comparatively wide funnel-shaped opening into the cavity of the thirteenth segment, and extending backwards and outwards in the fourteenth segment to open at the female aperture on the ventral surface of the latter. The *receptacula ovorum* are a pair of reniform sacs which open into the funnel-shaped ends of the oviducts. The *receptacula seminis* or *spermathecæ* (*rec.*) are two pairs of rounded sacs which open on the exterior in the intervals between the ninth and tenth and tenth and eleventh segments.

Though hermaphrodite, the Earthworm is not self-fertilizing, but two

individuals provide for mutual fertilization by an act of copulation. The copulating individuals apply themselves together by their ventral surfaces, the heads pointing in opposite directions, and become attached in this position by the setæ of the genital region and by a viscid secretion from the clitellum and of the capsulogenous glands (p. 325), situated in the neighbourhood of the

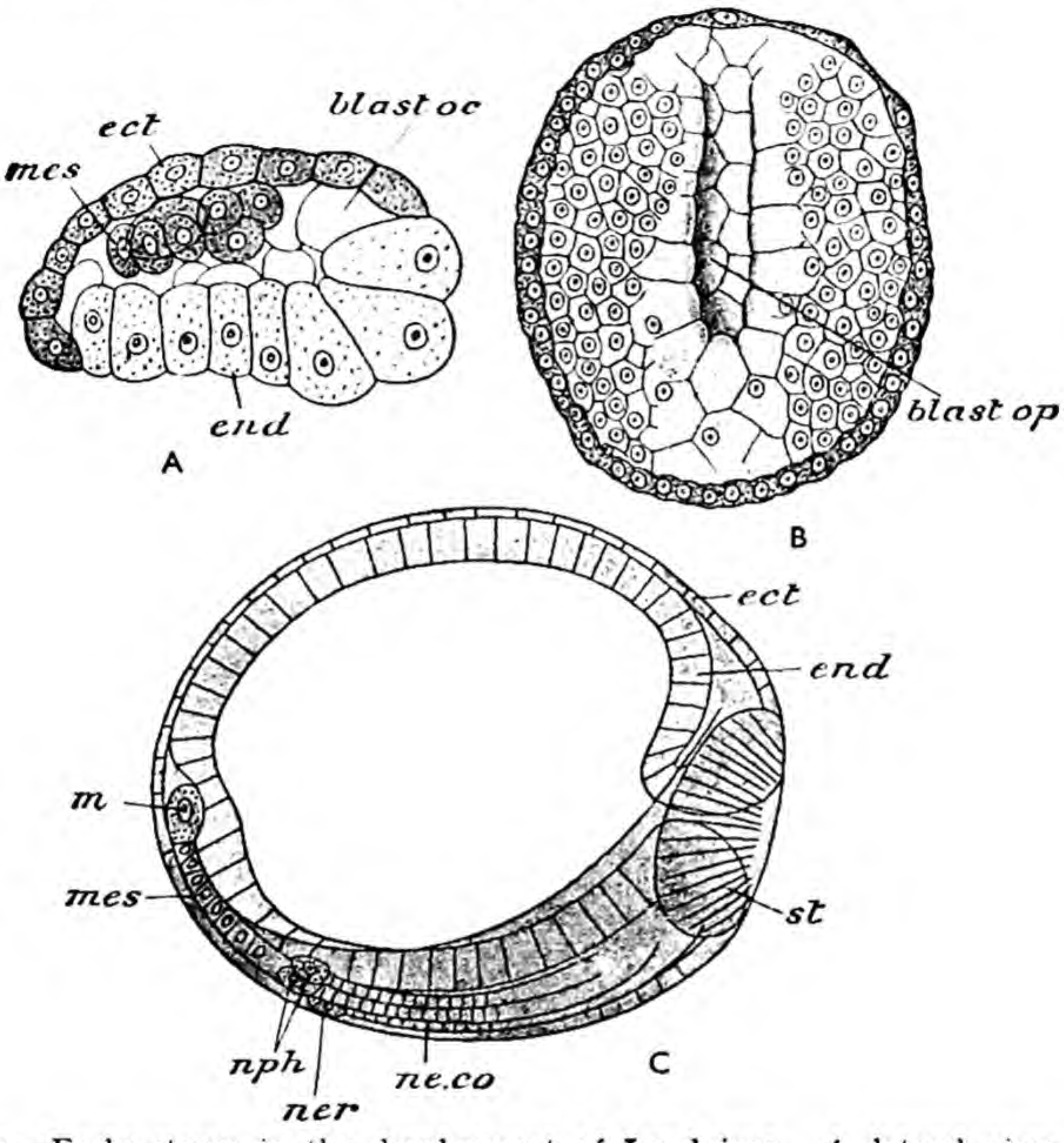


FIG. 295.—Early stages in the development of **Lumbricus.** *A*, lateral view of flattened blastula; *B*, ventral view of gastrula with slit-like blastopore; *C*, lateral view of later stage. *blastoc.* blastocœle; *blastop.* blastopore; *ect.* ectoderm; *end.* endoderm; *m.* primary mesoderm cell; *mes.* mesoderm bands; *ner.* cell from which the primitive nerve-cord (*ne. co.*) takes origin; *nph.* cells taking part in the formation of the nephridia; *st.* stomodæum. (After Wilson.)

reproductive organs. The sperms from the male apertures of each pass along temporarily formed grooves to the *receptacula seminis* of the other.

When the ova are mature they are discharged from the ovary into the cavity of the thirteenth segment, whence they pass out to the exterior through the oviducts, to be enclosed in the cocoon (*vide infra*), after having being detained for a time in the receptacula ovorum.

Development.—The fertilized ova of the Earthworm are enclosed, together with a quantity of an albuminous fluid derived from the capsulogenous glands,

in a *cocoon*, the wall of which is formed of a viscid secretion from the glands of the clitellum, hardened and toughened by exposure to the air. The cocoon is deposited in the earth and the embryos develop into complete, though minute, worms before they make their escape. The cleavage is unequal and of the spiral type. A flattened *blastula* (Fig. 295, *A*) is formed, with a large but flattened blastocœle. This forms a cylindrical *gastrula* (*B*); the blastopore narrows and subsequently gives rise to the mouth of the adult. A pair of large *mesoderm* cells are early marked off from the other cells of the gastrula; these undergo division to form a pair of *mesoderm bands* (*C*, *mes.*) composed of several rows of small cells which grow forwards towards the mouth. By swallowing movements the embryo at this stage, having burst through the enclosing vitelline membrane, takes in the albuminous fluid in the interior of the cocoon, and increases rapidly in size. As the embryo elongates, the mesoderm bands become divided into segments, and the subsequent history of these is essentially similar to what has been already described in the case of Nereis. The ectoderm is thickened on each side along the line of the mesoderm bands, and the mass of ectoderm cells so formed becomes arranged in a number of rows each originating behind in a larger rounded cell or *teloblast*. The innermost of these rows (Fig. 295, *C*, *ner*, *ne. co.*) give rise to the ventral nerve-cord. The next two rows (*nph.*) are said by some observers to give rise to the nephridia all but the funnels; but according to others the nephridia, or at least all their inner glandular portions, are of mesodermal derivation. The brain and œsophageal connectives are formed in continuity with the rudiments of the ventral nerve-cord.

On the whole the development resembles that of Nereis, the chief differences being such as may be traced to the non-occurrence in the Earthworm of any free-swimming trochophore stage, with the absence of such larval structures as the large pre-oral lobe, the apical plate, the prototroch, and the larval nephridia.

2. Distinctive Characters and Classification.

The Chætopoda are Annelida with the body made up of distinct metameres, which are usually numerous and similar throughout. The metameres are provided with chitinous setæ developed in sacs (setigerous sacs) of the epidermis, and usually elevated on muscular appendages, the parapodia. There is a large cælome divided internally into chambers by transverse septa, and not in communication with the blood-vascular system, which is nearly always highly developed. The ventral nerve-cord consists of a chain of ganglia. The reproductive cells are formed by a proliferation of certain parts of the peritoneum or membrane lining the cælome, and usually reach the exterior through cælomoducts or through modified or unmodified nephridia.

ORDER I.—POLYCHÆTA.

Chætopoda with the sexes distinct, and the ovaries and testes of simple character and metamerically repeated. Highly developed parapodia are present, in most instances, bearing numerous long setæ. There is usually a definite head with eyes and tentacles, and often cirri and branchiæ on the segments of the body. A clitellum is never developed. A metamorphosis takes place: the larva is a trochophore. Nearly all the Polychæta are marine.

Sub-order a.—Errantia.

Polychæta with protrusible pharynx usually armed with chitinous jaws. There is a well-developed head. The segments are completely or nearly similar throughout the length of the body, and the parapodia are usually equally developed throughout and provided with cirri. The branchiæ, when present, are not confined to the anterior end. The members of this sub-order are prevalently free-swimming, often pelagic; some live temporarily in tubes.

Examples: *Euphrosyne, Aphrodite, Polynöe* (Fig. 296), *Phyllodoce* (Fig. 302), *Alciopa* (*pelagic*), *Tomopteris* (*pelagic*), *Hesione, Syllis* (Figs. 302, 313), *Pionosyllis* (Fig. 309), *Autolytus* (Fig. 312), *Nereis* (Fig. 277), *Nephthys* (Fig. 302), *Glycera, Eunice* (Fig. 302), *Histriobdella, Stratiodrilus* (Fig. 314).

Sub-order b.—Sedentaria.

Polychæta devoid of protrusible pharynx and of jaws or teeth. The head is frequently very small, and sometimes is devoid of eyes or tentacles, the prostomium sometimes much reduced and covered over by the peristomium. The body is distinguishable, by differences in the form of the segments, parapodia, and setæ, into two or even three regions. The parapodia are little prominent in the posterior parts, and usually without cirri. The branchiæ, when present, are usually confined to the anterior end, and are sometimes represented by modified cephalic palpi. The members of this sub-order live in tubes which they rarely or never leave; some burrow in the sand.

Examples: *Chætopterus* (Fig. 298), *Polydora and Trophonia* (*Stylarioides*), *Polyophthalmus, Dasybranchus, Arenicola, Sternaspis, Terebella* (Fig. 304), *Sabella, Dasychone, Fabricia, Galeolaria* (Fig. 297), *Serpula* (Fig. 315), *Pomatoceros, Spirorbis* (Fig. 310).

ORDER 2.—OLIGOCHÆTA.

Chætopoda with the sexes united, the reproductive system complicated, the ovaries and testes compact and never more than two pairs of each. No definite paropodia are developed and no cirri, and only a small number of simple setæ on each segment. The head is not distinct. A clitellum is usually present. There is no metamorphosis. Mostly terrestrial or fresh-water forms. The numerous families of the Oligochæta can be subdivided according to their habitat into two groups: The *Earthworms* and the *Aquatic Oligochæta*.

The **Earthworms** are mostly large Oligochæta with many segments, never multiplying asexually. The male genital pores are behind the seventh segment. The vasa deferentia are elongated, passing through two or more segments. The anterior part of the body is never specialized as regards its setæ. The clitellum, which consists of two layers of cells, never begins in front of the twelfth segment. Eye-spots are not developed.

Example: *Lumbricus* (Fig. 288).

The **Aquatic Oligochæta** are mostly small worms with relatively few segments, often multiplying asexually. The male genital pores are on, or in front of, the seventh segment. The vasa deferentia are short, opening on the segment immediately behind that in which the internal apertures are situated. The anterior part of the body is often distinguished

from the rest by a difference in the form and arrangement of the setæ. The clitellum, which is composed of only one layer of cells, is situated comparatively far forward. Eye-spots are frequently present.

Examples: *Nais*, *Chætogaster*, *Tubifex* (Fig. 303).

3. General Organization.

The **general form of the body** in the Chætopoda is cylindrical, but in many, *e.g.* some members of the families *Polynoidæ* (Fig. 296) and *Amphinomidæ*, there is a very considerable degree of dorso-ventral compression. In most the body is very long in comparison with its breadth; but this is not a universal rule, the length being in some cases not more than five or six times the breadth. The surface is marked out by a number of more or less distinct annular constrictions or impressed lines into a corresponding series of *segments* or *metameres*, which are usually very numerous, often some hundreds in number, though in some cases there are not more than from twenty to thirty. These segments are usually very similar throughout the length of the body; but in the Sedentaria (Figs. 297, 298, 304) there may be two or even more regions distinguishable from one another by the form of the segments and of their appendages. In the Oligochæta there is a thickened zone, the *clitellum*, comprising sometimes only one segment, sometimes a number. Each segment, with certain exceptions to be noted presently, bears either a pair of *parapodia* or merely a greater or smaller number of setæ. Parapodia are lateral hollow processes of the body-wall bearing a number of bristles or setæ Frequently the parapodium is divided horizontally into two distinct lobes or branches—a dorsal which is termed the *notopodium*, and a ventral which is termed the *neuropodium*. Even when this is not the case there may be two bundles of setæ representing the two parts. The setæ are nearly always chitinous; in *Euphrosyne* they are calcified. They are always solid, except in *Euphrosyne*, entire, or divided into a number of joints. In shape (Fig. 299) they vary greatly in different groups; often several very distinct forms of setæ are present in different parts of each parapodium of a single worm, or in parapodia of different regions of the body. Some are exceedingly delicate and hair-like, others needle-shaped, others compressed and sabre-like, others bayonet-like. Very often there is a long, straight, narrow part or handle with which is articulated a terminal blade, or bayonet, or hook. Sometimes the setæ are quite short, projecting little beyond the parapodia, and are hook-like or comb-like. Usually each bundle contains, in addition to the ordinary setæ, a stouter, straight,

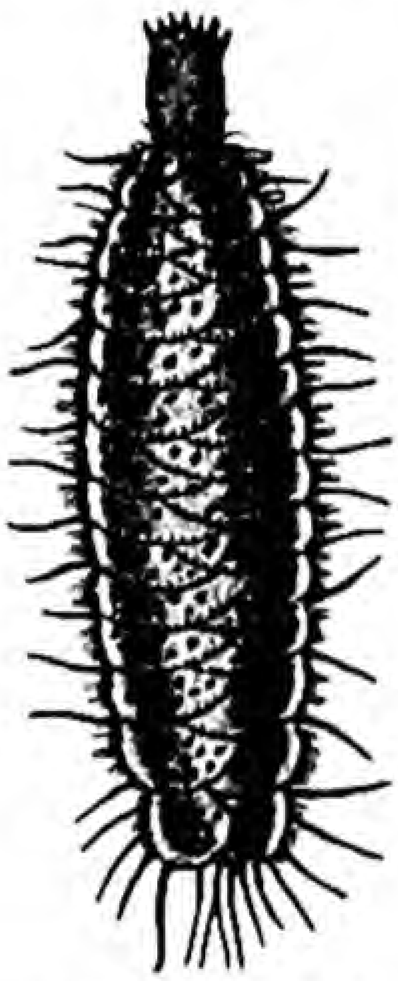


Fig. 296.—**Polynöe setosissima.** Dorsal view of entire animal, with the pharynx protruded. (After Quatrefages.)

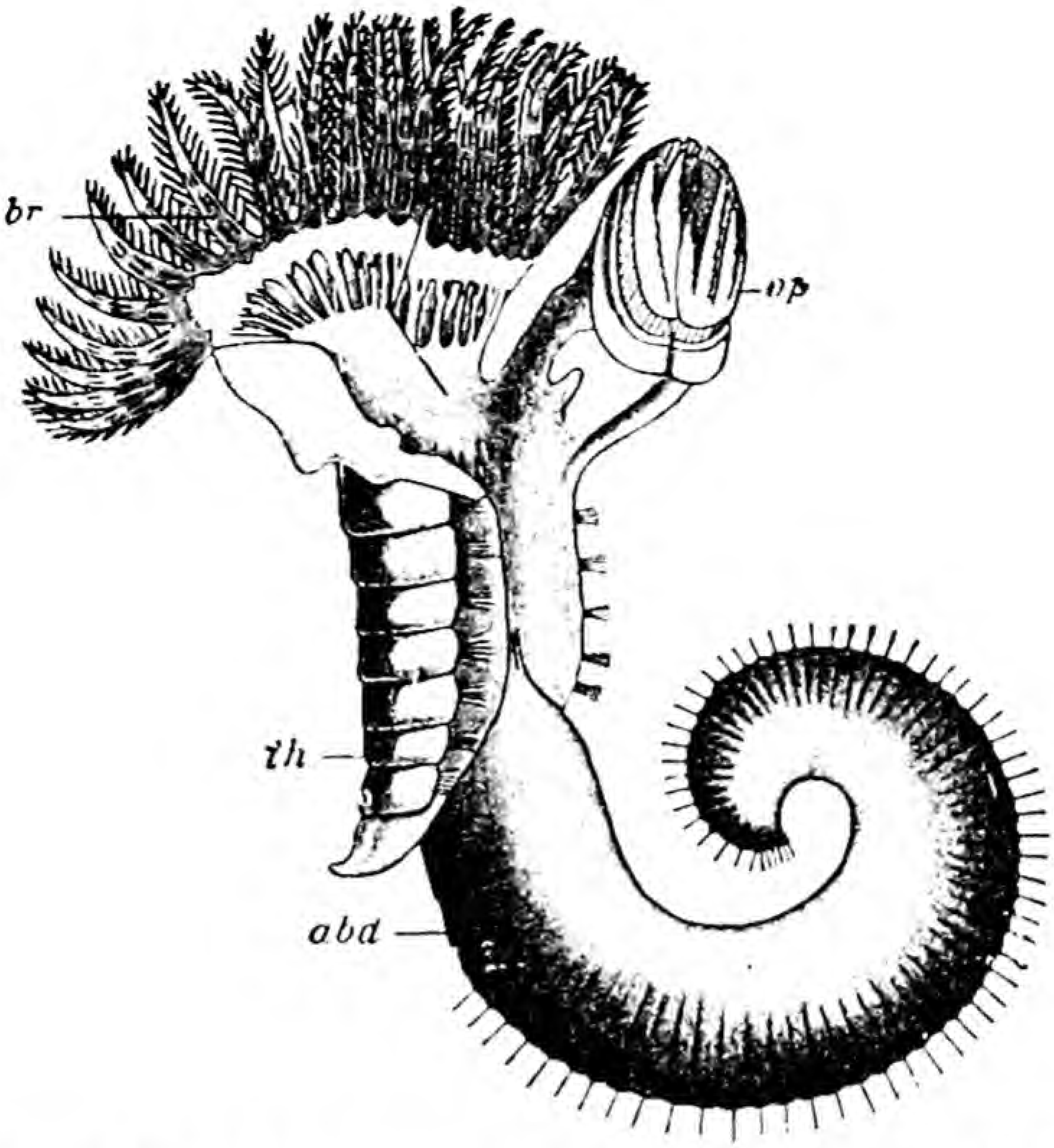


FIG. 297.—**A Serpulid** (Galeolaria cœspitosa). Lateral view of animal removed from its tube. *abd.* abdomen; *br.* branchiæ; *op.* operculum; *th.* thorax.

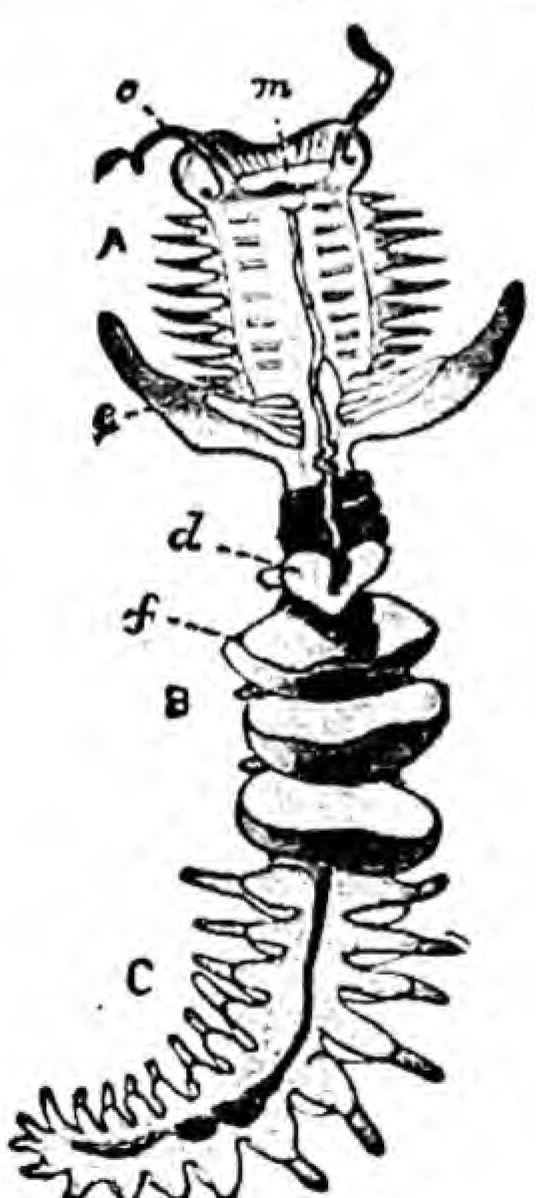


FIG. 298.—**Chætopterus.** Natural size of a young specimen. *A*, anterior region of the body; *B*, middle region; *C*, hinder region. *c*, peristomial cirri; *d*, "sucker"; *e*, the great "wings"; *f*, the first of the three "fans"; *m*, mouth. (From Benham, after Panceri.)

FIG. 299.—Setæ of various Polychæta. (From Claparède.)

simple seta, which scarcely projects on the surface; this is termed the *aciculum*. Each seta, or each bundle of setæ, is lodged in a sac, the *setigerous sac* (Fig. 300), formed by an invagination of the integument, and lined by cells continuous with the epidermis. Each seta is derived from one of these cells, and is to be looked upon as a specially developed part of the cuticle of the general outer surface. The setigerous sacs are usually provided with protractor and retractor muscles, by the action of which the setæ may be thrust out or retracted.

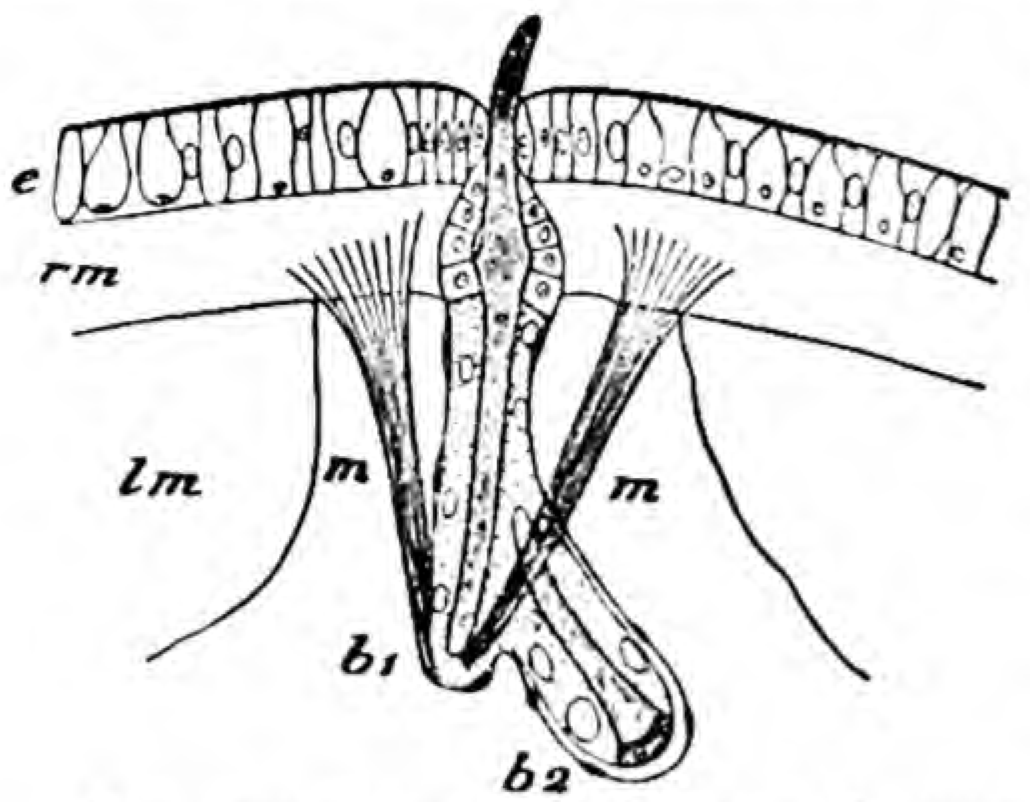


FIG. 300.—Section of the setigerous sac of an Oligochæte. b_1, setigerous sac; b_2, supplementary follicle with seta; *e*, deric epithelium (epidermis); *lm*. longitudinal muscles of body-wall; *m*, *m*. muscles of the setigerous sac; *r. m*. circular muscular layer of body-wall. (From Hatschek, after Vejdovsky.)

In addition to the setæ the parapodium bears very commonly certain soft appendages of a sensory character, the *cirri* (Fig. 278, *dors. cirr.*, *vent. cirr.*). There are usually both dorsal and ventral cirri, the latter nearly always much smaller than the former. The cirri are usually filamentous, sometimes jointed; sometimes they are laterally compressed and leaf-like. In *Polynöe* (Figs. 296 and 301)

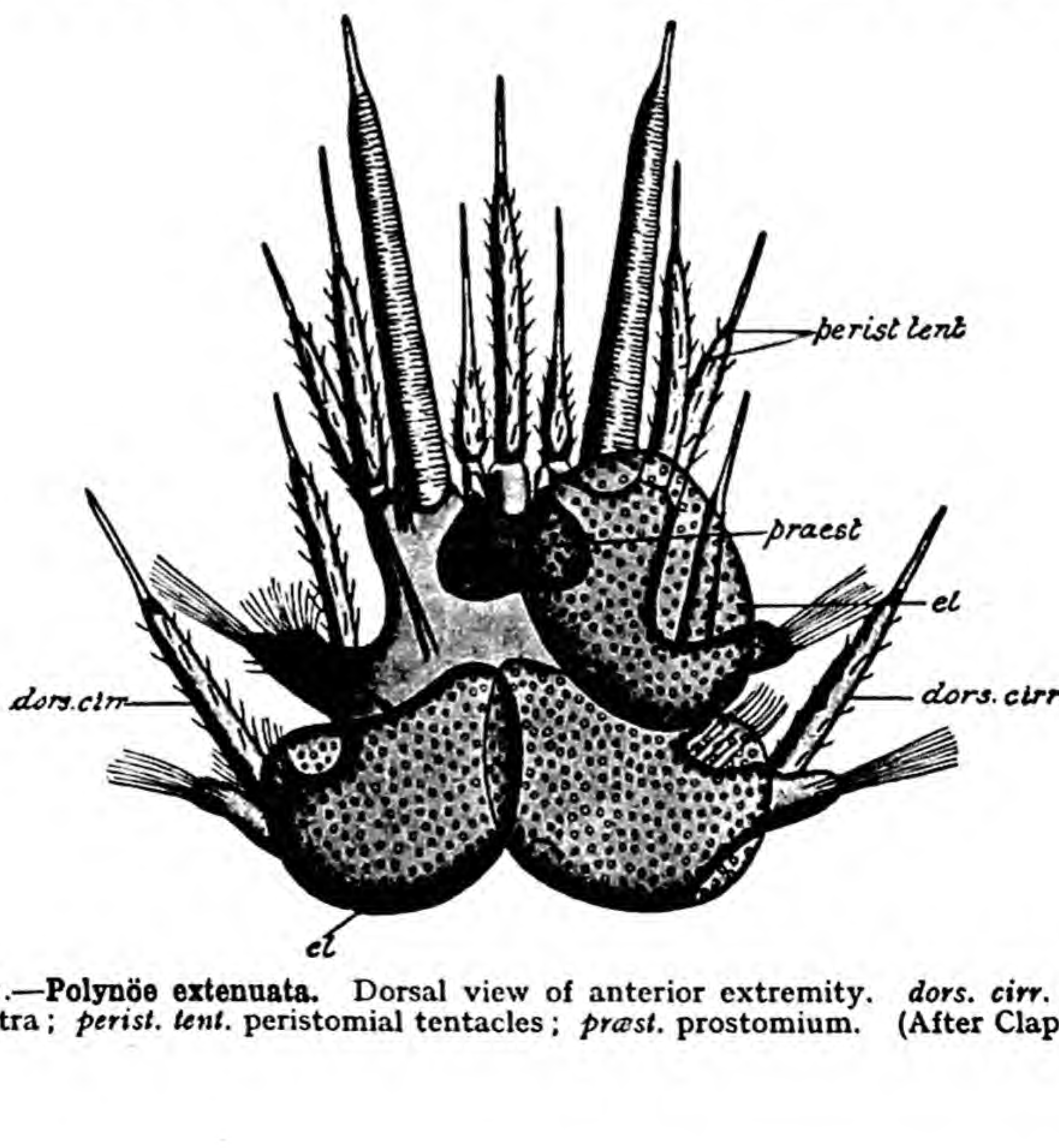


FIG. 301.—Polynöe extenuata. Dorsal view of anterior extremity. *dors. cirr.* dorsal cirri; *el.* elytra; *perist. tent.* peristomial tentacles; *præst.* prostomium. (After Claparède.)

and its allies certain of the parapodia bear, instead of dorsal cirri, flattened scales, the *elytra* (*el.*), richly supplied with nerves: these are sometimes looked upon as modified dorsal cirri, but in some members of the group cirri and elytra occur together on the same segment.

In *Sternaspis* a ventral shield formed by a thickening of the cuticle in the posterior region of the body bears a number of setæ round its edge.

In the Oligochæta (Fig. 303) the parapodia are absent as processes of the

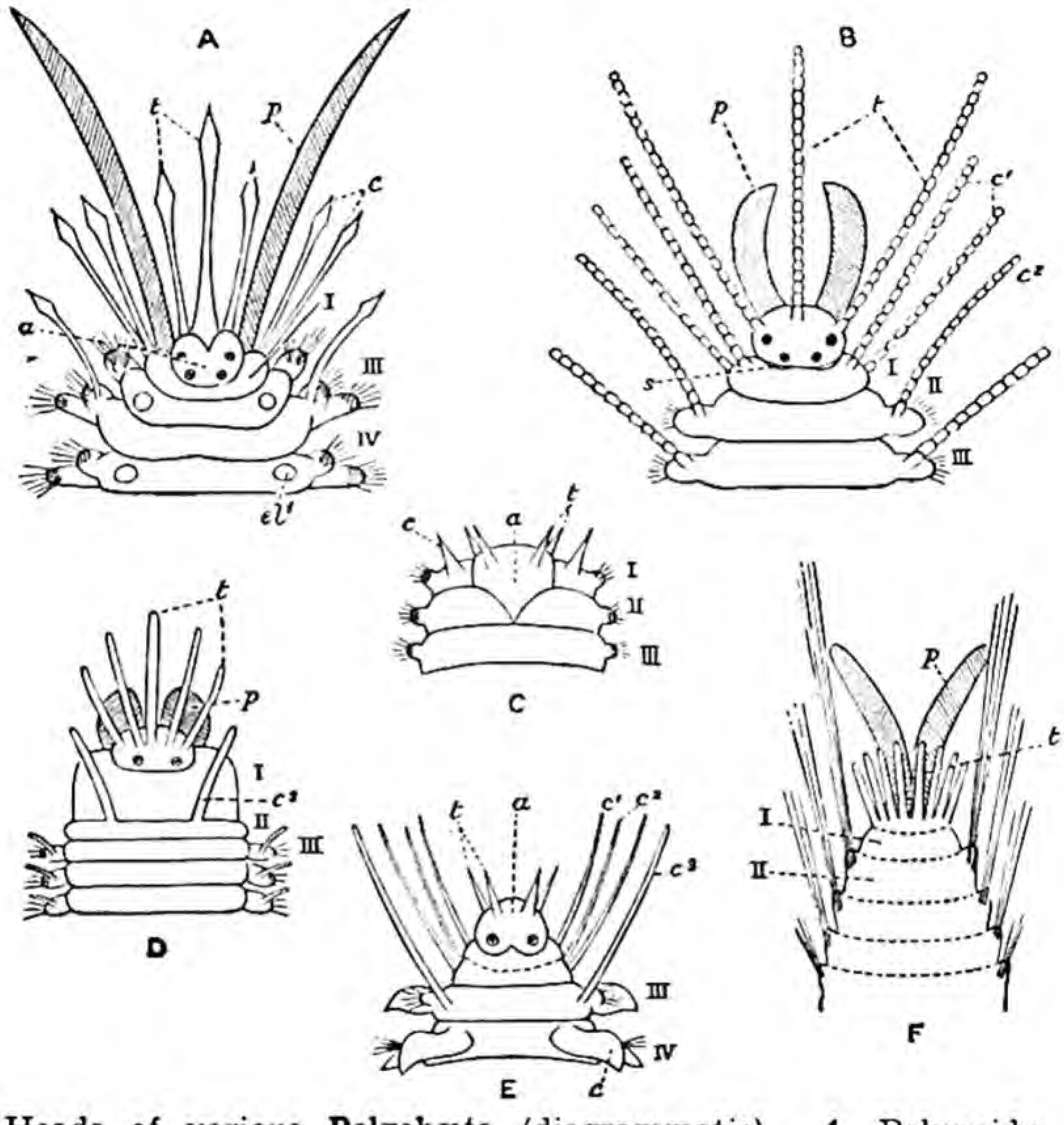


FIG. 302.—Heads of various **Polychæta** (diagrammatic). *A*, Polynoid; *B*, Syllid; *C*, *Nephthys*; *D*, *Eunice*; *E*, *Phyllodoce*; *F*, *Trophonia*. *a*, prostomium; *c*, cirri of body-segments; c^1, peristomial cirri (tentacles); c^2, cirrus of first body-segment; c^3, cirrus of second body-segment; *el'*, point of attachment of elytron; *p*, palp; *s*, nuchal organ; *t*, tentacle; *I*, peristomium: *II*, *III*, *IV*, segments. (From the *Cambridge Natural History*.)

body-wall, and are merely represented by a small number of short setæ each lodged in its sac; cirri are not developed. In certain Oligochæta setæ are absent.

The first segment or *prostomium*, together with the second or *peristomium*, forms in many Polychæta a very distinct head; the prostomium in such a case bears eyes and tentacles and contains the cerebral ganglion; on the peristomium is the opening of the mouth, and from it also arise the *peristomial tentacles*. A ventral pair of prostomial tentacles, somewhat thicker than the rest, are sometimes to be distinguished, and are termed the *palpi*. Neither

FIG. 303.—**Tubifex.** General view of entire animal. (After D'Udekem.)

prostomium nor peristomium bears parapodia, though an aciculum is sometimes developed in the latter; the prostomium, in fact, is not quite correctly termed a segment, being different from the true segments both in structure and in mode of development. In the Oligochæta there is no definite head, tentacles are entirely absent, and in the terrestrial forms the prostomium does not lodge the cerebral ganglion. In *Sternaspis spinosa* the prostomium is elongated and bifurcated like the proboscis of the *Echiurida* (*vide infra*).

The last segment is termed the *anal segment*, owing to its bearing the anal opening; it usually also differs from the preceding segments in wanting the parapodia and in having a pair of special cirri, the *anal cirri*.

Branchiæ are borne on the dorsal surfaces of more or fewer of the segments in many of the Polychæta. Sometimes they occur on all, or nearly all, the segments; sometimes they are confined to the middle region of the body; sometimes they are present only at the anterior end, as in the majority of the Polychæta living habitually in tubes (Figs. 297 and 304). In the *Terebellidæ* (Fig. 304) the branchiæ are situated on the dorsal surfaces of some of the anterior segments. In the *Serpulidæ* (Fig. 297) they form two incomplete lateral circlets of elongated appendages situated at the anterior end of the body, apparently representing modified palpi, and sometimes supported by a cartilaginous skeleton; one of them is enlarged to form a stopper or *operculum* (*op.*), often armed with calcareous plates and spines, for the closure of the mouth of the tube in which the Annelid lives. In shape the branchiæ are sometimes filiform, sometimes compressed and leaf-like, sometimes branched in a tree-like manner,

sometimes pinnate. In *Serpula* (Figs. 297 and 315) and its allies each branchia consists of an elongated stem on which are borne two rows of short filaments. The surface of the branchiæ is usually ciliated. They are richly supplied with blood-vessels when a blood-vascular system is developed; in *Glycera*, in which there are no blood-vessels, each branchia contains a diverticulum of the cœlome.

In the Oligochæta branchiæ are rarely present; but in certain of the

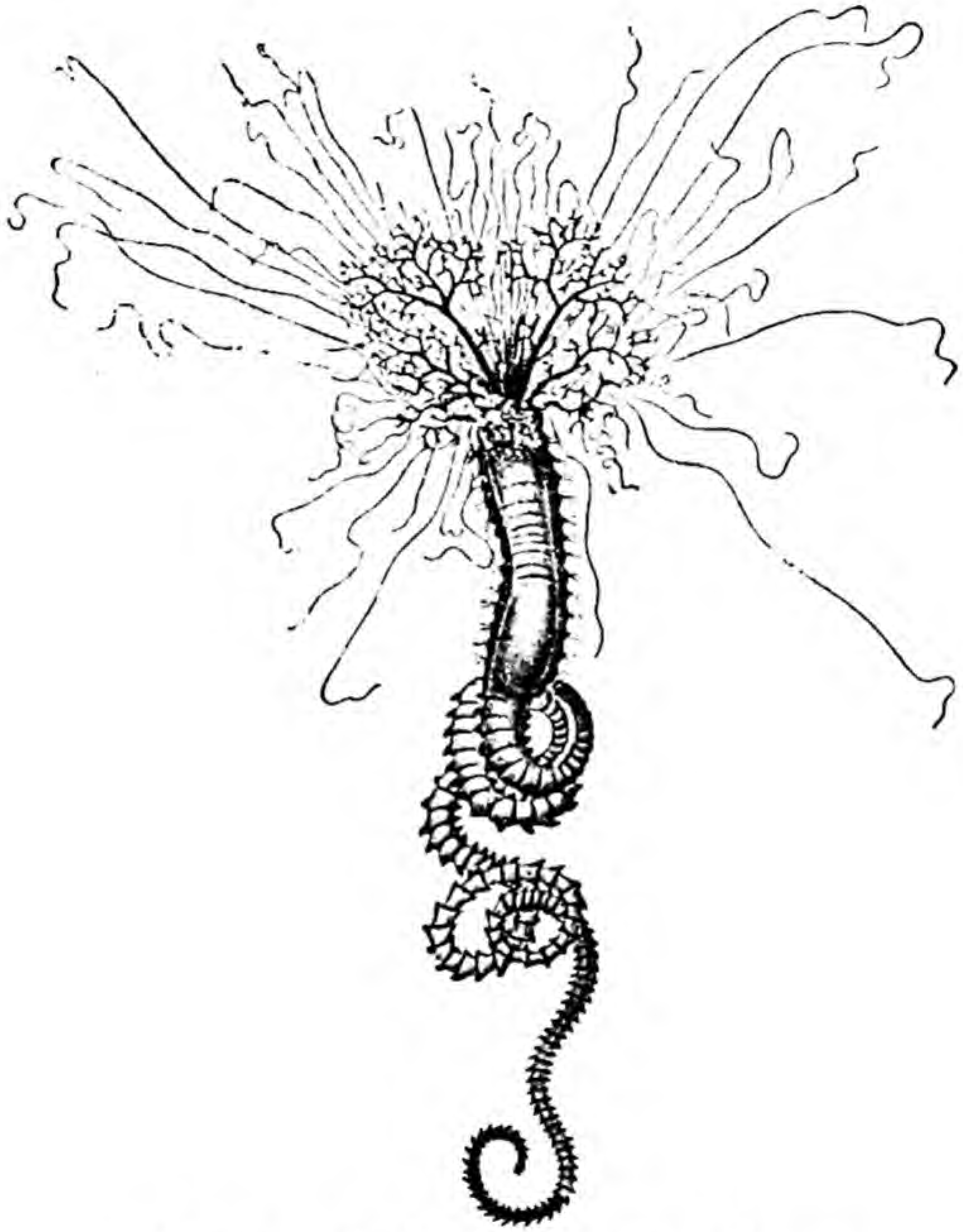


FIG. 304.—**Terebella.** (After Quatrefages.)

aquatic Oligochæta there are metamerically arranged simple or branched branchiæ, sometimes retractile, on the segments of the posterior region.

The **body-wall** consists of a cuticle, an epidermis, muscular layers, and a layer of peritoneum. The *cuticle*, composed of a chitinoid material, usually presents two systems of fine lines intersecting one another at right angles: it is perforated in many places by the ducts of the unicellular glands of the epidermis. The epidermis consists of a single row of cells, in some cases with smaller cells of replacement intercalated between their inner ends. In shape

the cells vary greatly in different families and often in different parts of the body of the same worm, being sometimes flattened, sometimes cubical or polyhedral, but more usually more or less vertically elongated. Cilia occur on the surface in certain parts in many Chætopoda. Among the ordinary cells of the epidermis there are usually numerous unicellular glands often containing rod-like bodies. In the tubicolous forms these unicellular glands are active in secreting the material for the construction of the tube. In addition, the epidermis frequently contains sensory cells, which are in many cases contained in certain special elevations or sensory papillæ.

The *muscular* part of the body-wall consists of two layers, in the outer of which the fibres are disposed circularly, while in the inner their arrangement is longitudinal. The circular layer is continuous, or, more usually, is interrupted opposite the intervals between the segments. The longitudinal layer is disposed in four bands in the Polychæta, two dorso-lateral and two ventro-lateral. In the Oligochæta, it is divided by the setigerous sacs which pass through it.

The *peritoneal* or *cœlomic epithelium* consists of a single layer of cells. These are usually non-ciliated, but are ciliated in *Aphrodite*, in *Glycera*, and some others, the movement of the cilia bringing about an active circulation of the *cœlomic* or *perivisceral fluid* in the cœlome.

The **body-cavity** or **cœlome,** a wide space intervening between the wall of the body on the one hand and that of the enteric canal on the other, is divided in many Chætopoda by a series of transverse septa into a series of chambers corresponding to the segments. The septa are not complete partitions, there being always apertures of greater or less extent by which the cavities of neighbouring segments communicate. The septa consist of double folds of the peritoneum enclosing muscular fibres.

The **enteric canal** is an elongated and nearly always straight tube, running through the entire length of the body from mouth to anus. A number of different parts are usually distinguishable; but their disposition varies to a very great extent in the different groups. The buccal cavity, into which the mouth leads, is followed by a muscular pharynx; these are both formed in the embryo by invagination of the ectoderm, and therefore correspond to a *stomodæum*. The muscular pharynx is absent in some of the Sedentaria: when present it is frequently protrusible to a greater or less extent (see Figs. 280, 296); around its extremity, when it is fully protruded, are to be seen a circlet of papillæ in some forms; and in many, one or more horny teeth, situated in its interior, are brought into play. A *gizzard* with thick walls may follow upon this protrusible pharynx, and is sometimes preceded by an *œsophagus*, which may be dilated behind into a *crop*. The *intestine* is nearly always more or less deeply constricted inter-segmentally, and in *Aphrodite* (Fig. 305), there are in each of the segments (with the exception of one or two of the most anterior and one or two of the most posterior) a pair of *cæca* which are

to a greater or less extent branched at their extremities. In the *Hesionidæ* a pair of cæca which open into the anterior part of the intestine frequently contain gas, and probably have a hydrostatic function. In some of the terrestrial Oligochæta (Earthworms) a fold of the intestinal wall, the *typhlosole*, projects into its lumen. The intestine is straight in most, but is somewhat coiled in *Sternaspis*, and others. The wall of the alimentary canal consists (1) of the visceral layer of peritoneum; (2) of longitudinally arranged muscular fibres; (3) of circularly arranged muscular fibres; (4) of enteric epithelium. The peritoneum on the surface of the intestine has in many Chætopoda its cells enlarged and granular to form the so-called *chloragogenous cells*, which probably have an excretory function. The enteric epithelium is very generally ciliated; it contains numerous gland-cells. The stomodæum and the proctodæum are lined internally by a cuticular layer, which is continuous with the cuticle of the general surface. The anus is usually terminal in position, sometimes directed towards the dorsal aspect. There is, in most instances, a longitudinal mesentery running to the alimentary canal from the dorsal body-wall; sometimes a ventral mesentery is also present bearing a corresponding relation to the ventral surface.

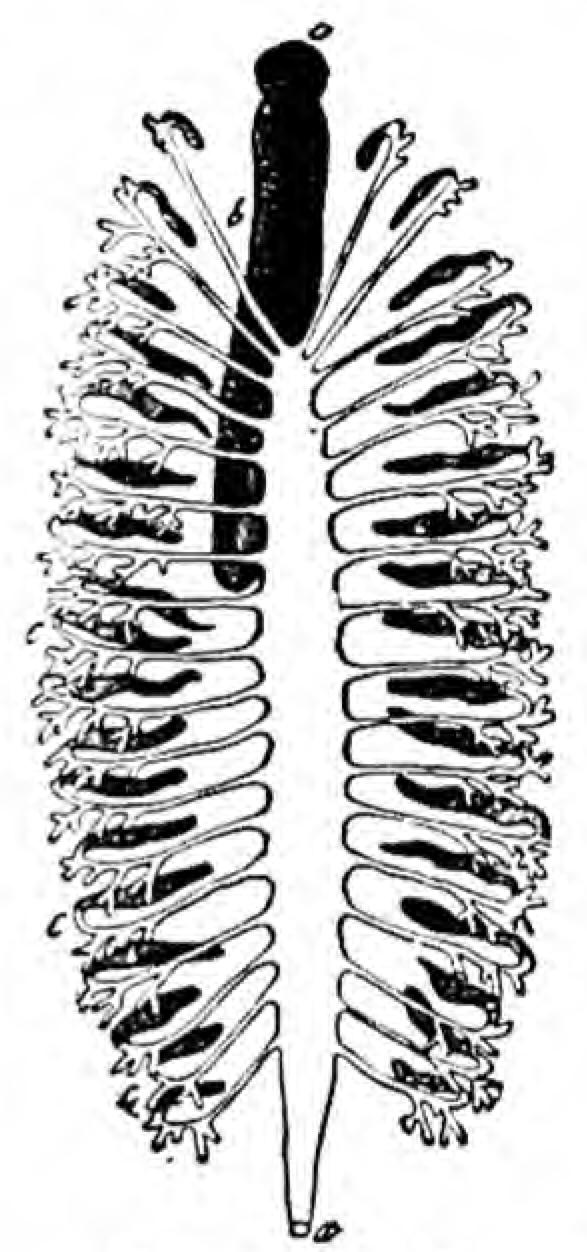


FIG. 305.—Enteric canal of **Aphrodite.** *a*, mouth; *b*, pharynx; *c*, branching cæca of intestine; *d*, anus. (From Gegenbaur's *Comparative Anatomy*.)

Some Chætopoda are entirely devoid of **blood-vessels.** In one family in which this is the case (the *Glyceridæ* among the Errantia), the perivisceral fluid, which assumes some of the functions of the blood, contains numerous red corpuscles, the red colour of which is due to the presence of hæmoglobin. In the majority of the Chætopoda there is a highly developed vascular system. Sometimes the blood is colourless: very commonly it is bright red in colour, owing to the presence of hæmoglobin, which is not confined to the corpuscles, but is dissolved in the plasma. In Serpula and its allies the blood is bright green, owing to the presence of a green colouring matter (*chlorocruorin*), which has an affinity for oxygen similar to that possessed by hæmoglobin.

The chief blood-vessels are usually dorsal and ventral longitudinal trunks. These are connected together by metamerically arranged transverse branches. In some of the Sedentaria the dorsal vessel is not present in the greater part of the length of the body, its place being taken by a peri-intestinal sinus or a plexus of vessels lying in the wall of the alimentary canal. This gives off in front a short thick-walled dorsal vessel or "heart." The movement of the blood is effected in most instances by peristaltic contractions of the dorsal vessel, or of a peri-intestinal sinus or plexus, or of the "heart" given off by the

latter anteriorly, which have the effect of driving the blood from behind forwards. In some instances, as in the Earthworms and some Sedentaria, specially dilated lateral vessels are contractile, and by their pulsations bring about the circulation of the blood through the system of vessels. Plexuses of fine capillary vessels in the integument of various parts frequently aid in respiration, and are particularly well developed in certain forms in which definite organs of respiration are absent.

The **nervous system** consists of a cerebral ganglion or *brain* and a double *ventral chain* of ganglia. The cerebral ganglion is distinctly bilobed, and may be looked upon as composed of two intimately united ganglia. It is almost invariably situated in the prostomium, though placed a little farther back in the Earthworms; it gives off branches to the eyes and tentacles. From it there run backwards and downwards the paired *œsophageal connectives*, which embrace the anterior part of the alimentary canal between them, and below join the anterior end of the ventral chain of ganglia. The latter always exhibits indications of being made up of two lateral halves in the double character of the connecting commissures and frequently of the ganglia themselves. One of these double ganglia occurs in each segment, and from it a number of nerves pass out to the various parts of the segment. In certain Sedentaria (*Serpula* and others) the two halves of the chain are separated from one another by a wide space, across which transverse commissures pass between the ganglia. Connected with the cerebral ganglia, or with the œsophageal connectives, or with both, there is a system of delicate *stomatogastric nerves* passing to the walls of the anterior part of the alimentary canal. In the majority of the Chætopoda the cerebral ganglion and the ventral chain are separated from the epidermis; in some, however, the ventral chain is in contact with the epidermis. Running longitudinally through the ventral cord in many forms are certain *giant fibres* of very large size; they are simply greatly enlarged and modified nerve-fibres. Nerve-cells may be confined to the ganglia, or may be distributed over the entire surface of the ventral cord. *Giant nerve-cells* occur in some forms in certain regions. Small ganglia are found frequently in various peripheral parts, more especially at the bases of cirri or of sensory papillæ.

The **sense-organs** are *eyes*, *tentacles* and *cirri*, *nuchal organs*, and *statocysts*. *Eyes*, absent in the Oligochæta with a few exceptions and in some of the tube-forming Polychæta as well as in a few free forms of that order, are very general in their occurrence. Their structure, is, as a rule, very simple, but in some forms reaches quite a high grade of development. Usually they are confined to the prostomium, but *Polyophthalmus*, in addition to the prostomial eyes, has pairs of eye-like organs—probably light-producing (luminescent) organs—on many of the segments of the body. *Leptochone* has a pair on each segment, and in *Fabricia* there is a pair on the anal segment; while in many species of *Sabella* and all the species of *Dasychone* there are eyes on the branchial filaments.

Most usually the eye is (as in Nereis, Fig. 284) a spherical capsule with a wall composed of a single layer of cells, which are elongated on the inner side, *i.e.* the side turned towards the brain, while on the outer side they are usually flattened. The outer thin part of the wall of the capsule, or *cornea*, is sometimes united with the epidermis; when the two layers remain distinct, the outer one is the *outer cornea*, the inner the *inner cornea*. In many cases a thickening of the surface cuticle over the cornea forms a *cuticular lens*. The cells of the inner portion of the wall of the capsule form the elements of the *retina*; they are long narrow cells, sometimes composed of three distinct segments—(1) a clear *rod*, directed towards the central cavity; (2) a middle segment which is densely pigmented; and (3) a segment containing the nucleus of the cell and directed towards the brain or the optic ganglion, with which it is connected by a nerve-fibre. Frequently the second and third segments are not to be separately recognized, the whole of that part of the cell which contains the nucleus being densely pigmented. A refractive mass fills the interior of the capsule, and is sometimes distinguishable into a firmer outer part, the *lens*, and a more fluid inner part, the *vitreous body*. This refractive mass is often continuous with the cuticle externally, and internally may be in continuity with the rods. In some cases the structure of the eyes is very much simpler. The eyes on the branchial filaments of many tube-forming Polychæta consist each of a group of retinal cells having its own lens-like body and quite independent of the others; the eye is thus a *compound* one.

Nuchal organs or *ciliated pits* (Fig. 302, *B*, *s*) are very general in the Polychæta. They consist of a pair of special ciliated areas or pits on the head, eversible in certain cases.

Statocysts are only exceptionally present. They consist of capsules of ciliated cells, in the fluid contained in which there are one or several calcareous *statoliths*.

Tactile cells of the epidermis, with or without a projecting tactile hair or stiff cilium, are very common, especially on the prostomium in the Oligochæta and on the tentacles and cirri in the Polychæta. Groups of these are often aggregated together in *papillæ* or *goblet-bodies*, with special nerve-supply and often with a ganglion or a single nerve-cell at the base.

The **organs of excretion** of the Chætopoda are a series of segmentally arranged tubes, the *nephridia*, of which a pair as a rule occur in each of the segments of the body with the exception usually of a few at the anterior and a few at the posterior end. In its simplest form the nephridium is a curved tube, primarily ectodermal in origin, ciliated internally, opening on the exterior by a laterally-placed pore at the one extremity, and at the other ending in a ciliated funnel or *nephrostome*, which opens into the cœlome either of the same segment as that on which the external aperture is situated (most Polychæta) or of the segment in front (all or most Oligochæta, some Polychæta). The nephridia thus

in such cases effect a communication between the cœlome and the exterior, and serve to carry off waste-products which have passed into the cœlomic fluid; but in many instances the cells lining the tube are active in separating out such waste-matters, and are loaded with granules and concretions.

In many Polychæta, however, there is no ciliated cœlomic aperture, the tube ending blindly internally, such a blindly ending nephridium (Fig. 306) being frequently branched. On the inner extremities in such cases, or on other parts of the tube, are situated a number of peculiarly modified cells, the *solenocytes*, sometimes separate, sometimes united together in groups. Each of these is a rounded cell lying in the cœlome, and connected with the nephridium by a long, slender, tubular process: through the lumen of the process extends a single, extremely long, vibratile flagellum, which may be prolonged for some distance in the interior of the nephridium itself. The resemblance between these solenocytes and the flame-cells of Platyhelminthes will at once be recognized.

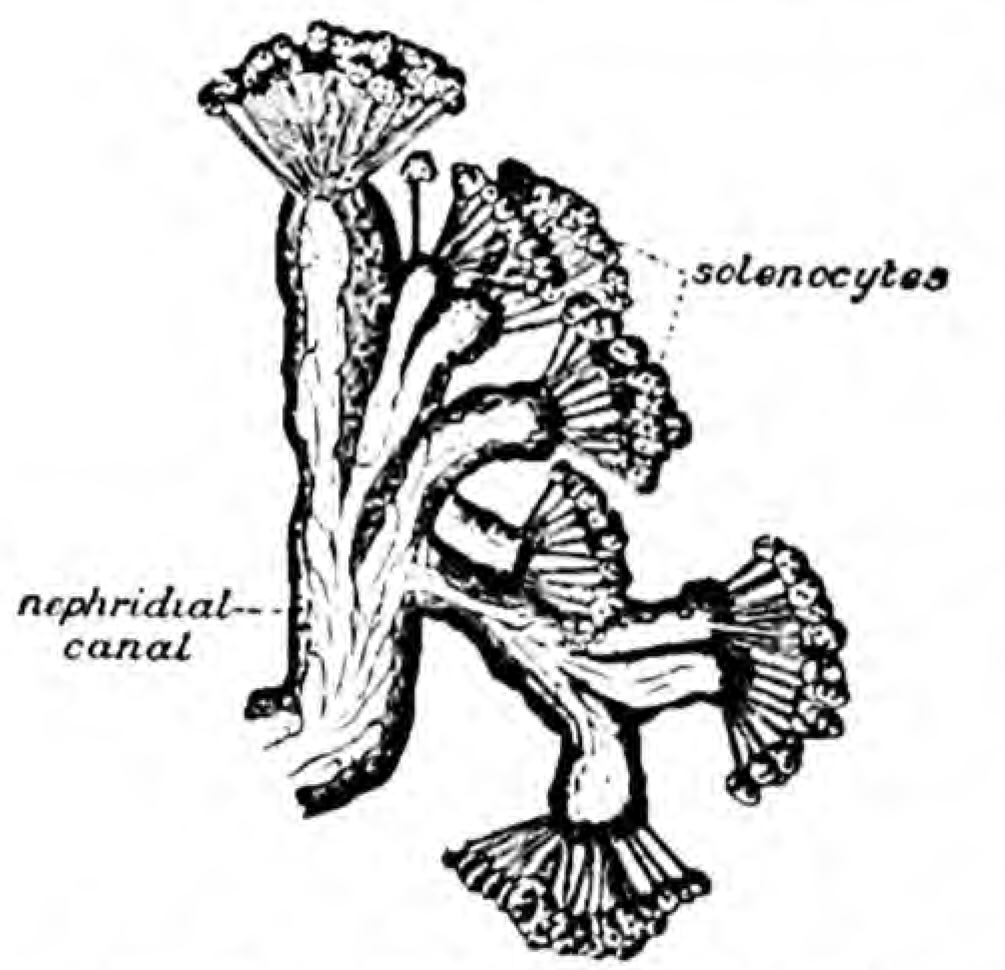


FIG. 306.—Inner branched end of nephridium of **Phyllodoce paretti**, showing the nephridial canal and the solenocytes. (After Goodrich.)

In the Polychæta another set of segmentally repeated structures are frequently intimately connected with the nephridia. These are a series of pairs of ciliated funnels, the *cœlomoducts*, opening widely into the cœlome, and, in a typical case, communicating with the exterior. In Nereis they are represented by the dorsal ciliated organ, and are not known to open externally. When provided with external apertures, as is usually the case, the cœlomoducts act as the efferent ducts for the sexual elements. In many of the Polychæta they do not remain independent, but coalesce partially or completely with the nephridia, and the functions of excretory organs and reproductive ducts become combined in the one set of " segmental organs " (Fig. 307). In some families of Polychæta (*Serpula* and allies) there is a single pair of large nephridia in the anterior region of the body, with smaller pairs in the posterior segments, the former alone appearing to have an excretory function, while the latter act exclusively as genital ducts. In *Sternaspis* only a single pair of nephridia are present, which, though they have small ciliated funnels, are not known to communicate with the exterior.

In the Oligochæta the nephridia are usually simple, elongated and coiled tubes, a pair or sometimes more than one pair in each segment; but, in some, these are replaced or supplemented in certain of the segments, or, in all, by a branching system of tubes with or without ciliated funnels. Sometimes the

ordinary nephridia are not developed in the segments lodging the reproductive organs, their place being there taken by three pairs of tubes of the nature of localized cœlomoducts which become modified to give rise to the reproductive ducts; but ordinary nephridia may be present in these segments as well. In some Oligochæta the nephridia of the most anterior segments open into the mouth or pharynx, and may have taken on the function of digestive glands (*peptonephridia*), and all the nephridia of the posterior region of the body in one species (*Allolobophora antipæ*), instead of opening on the exterior, communicate with a pair of longitudinal canals which posteriorly open into a median vesicle communicating with the rectum.

The permanent nephridia of the adult Chætopod are preceded in the larva by *provisional* or *embryonic nephridia* of a temporary character. These have been found to occur in the head (prostomium) of many larvel Oligochæta and Polychæta. They are ciliated intracellular tubes, sometimes branched, which do not open into the cavity of the prostomium. Sometimes solenocytes occur at the inner ends of the branches or of the undivided tube.

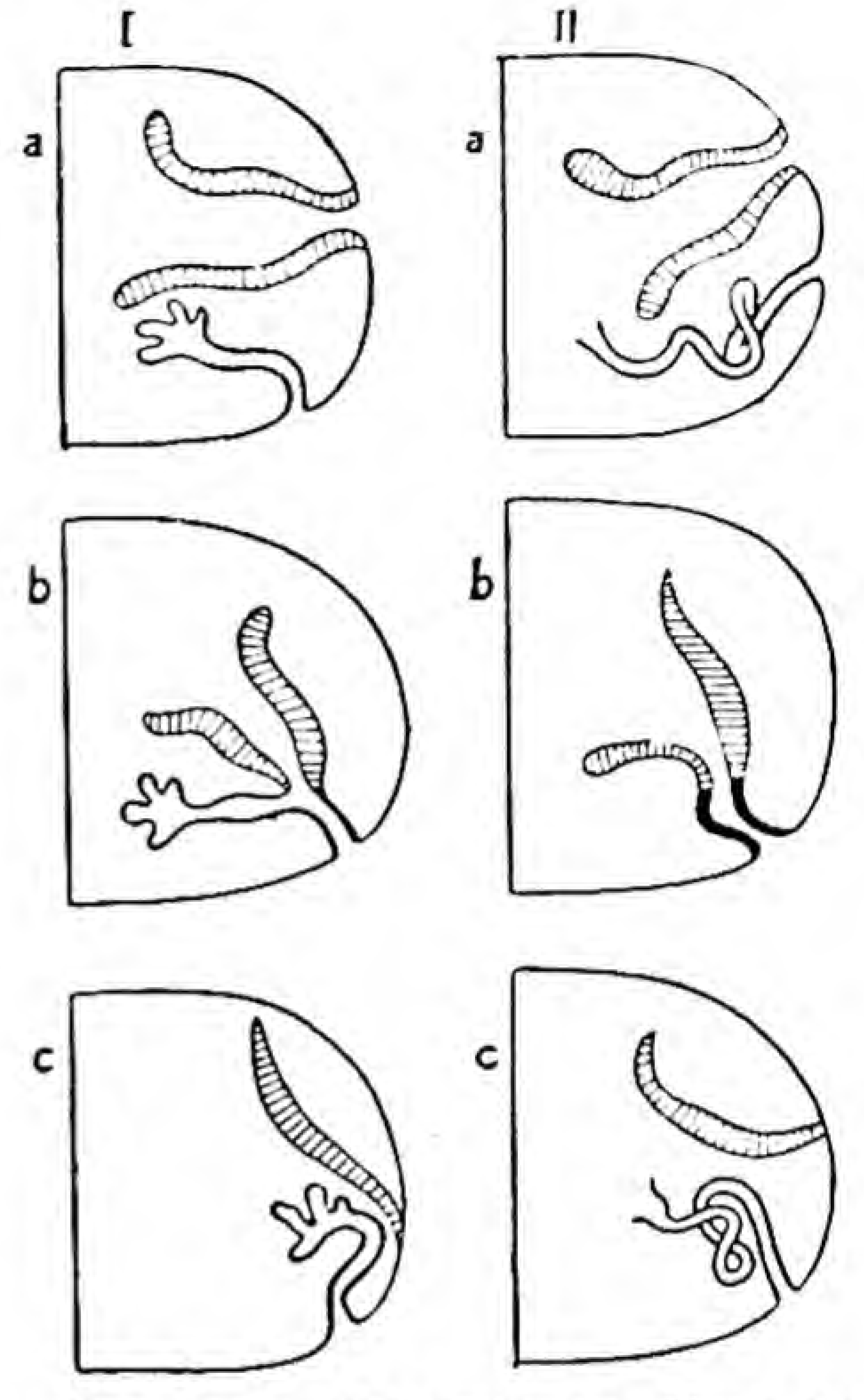


FIG. 307.—Diagram to illustrate the various combinations of closed and open **nephridia** and **cœlomoducts** in the Polychæta.

I*a*, Hypothetical stage with closed nephridia and separate cœlomoducts; *b*, condition in which the cœlomoducts have become united with the nephridia: this occurs in the *Phyllodocidæ* and *Goniadidæ*; *c*, condition in which the cœlomoduct becomes reduced to a ciliated organ (*Nephthyidæ*); II*a*, combination of nephridia with nephrostomes and separate cœlomoducts (*Dasybranchus*); *b*, condition in which "segmental organs" are formed by the union of nephridia with nephrostomes and cœlomoducts (the most usual condition); *c*, condition in which there are nephridia with nephrostomes, and the cœlomoducts are reduced to ciliated organs (*Nereis*, etc.). The nephridia are outlined with a thick line: the cœlomoducts striated. (After Goodrich.)

Luminescence, the production of light rendering the animal brilliantly luminous in the dark, occurs in a few cases (various Polynoids, *Chætopterus*, *etc.*). In some of these (*Polyophthalmus*) the light is produced by eye-like organs in most of the segments.

In the arrangement of the **reproductive organs** in the Chætopoda there is an essential difference between the two orders, the Oligochæta being hermaphrodite, and the Polychæta, with only a very few exceptions, unisexual. In the latter the *gonads*, ovaries or testes as the case may be, are masses of cells which are developed as the result of a proliferation of the cœlomic epithelium in certain positions (Fig. 308). Usually these organs,

which are only conspicuous about the breeding season, occur in the great majority of the segments of the body; sometimes they are confined to a certain region. The exact place which they occupy in the interior of the segment varies in different cases: sometimes they surround one of the principal blood-vessels, sometimes they are situated laterally, in the bases of the parapodia. The sperms frequently undergo the final stages of their development after they have become detached from the testes, while floating in the cœlomic fluid, and the same sometimes holds good of the ova. But sperms and ova appear to reach the exterior, in the majority of cases, through the "segmental organs,"

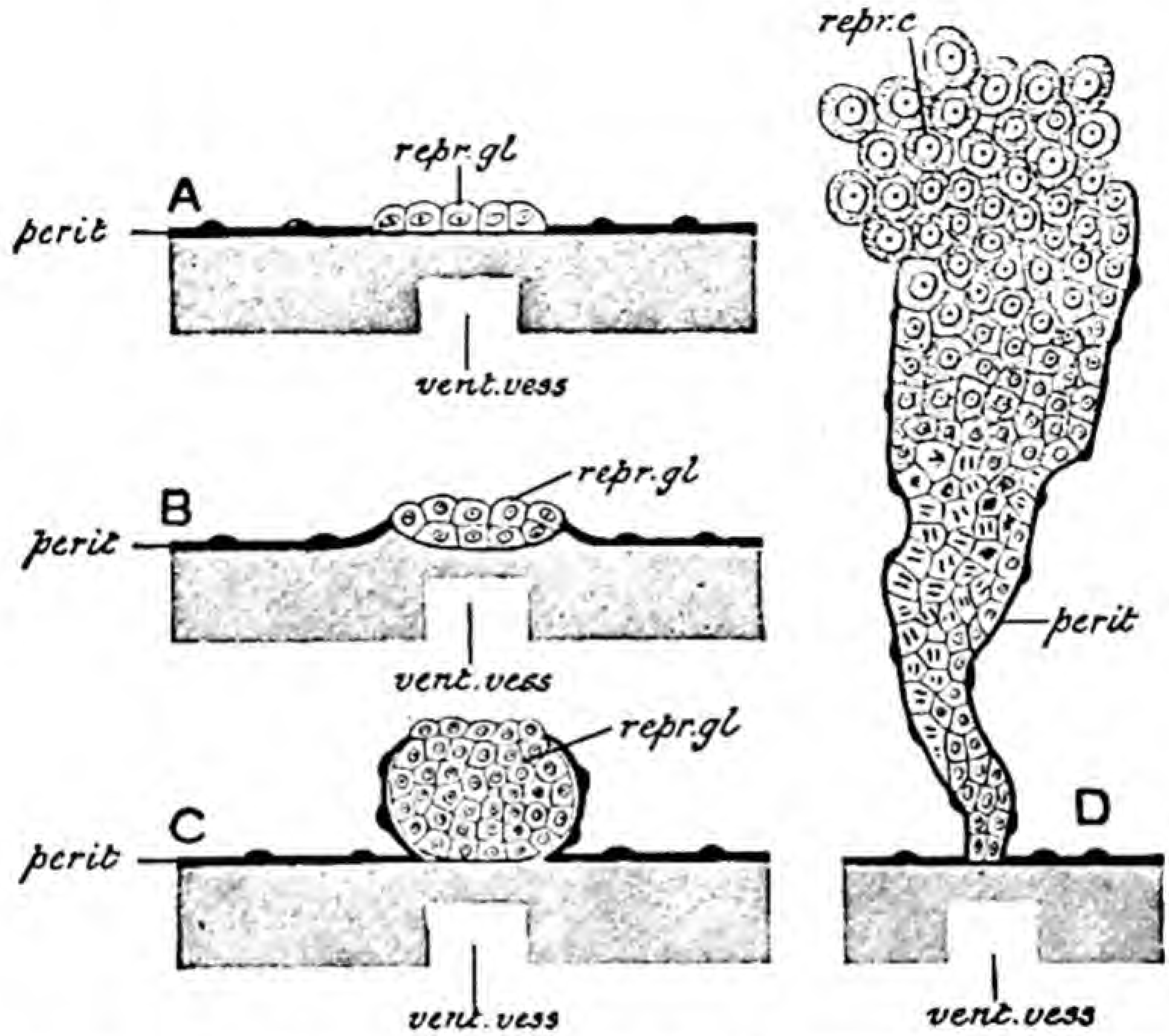


FIG. 308.—Diagram to illustrate the development of a gonad from the peritoneal (cœlomic) epithelium in one of the Polychæta. *perit.* peritoneal membrane; *repr. gl.* gonad (reproductive organ); *vent. vess.* ventral vessel. (After E. Meyer.)

which may become modified and enlarged at the breeding season, though in some forms it is stated that the reproductive cells escape through temporary or permanent openings in the body-wall. Fertilization takes place externally in nearly all.

In the Oligochæta the reproductive organs are confined to a certain limited region of the body. There are either, as in the Earthworms, two pairs of *testes*, or a single pair, as in the aquatic forms. The testes are small, and frequently become reduced to mere vestiges in the adult animal, having mainly become broken up into sperm-mother-cells, which in some way reach the vesiculæ seminales to undergo development into mature sperms. The *vesiculæ seminales* are comparatively large sacs, which vary in number and arrangement in the

different genera. One or two median *sperm-reservoirs*, formed by the coalescence of pairs of vesiculæ, may be present. In the same segments as the testes, and opening into the sperm-reservoirs when the latter are developed, are either two or four *ciliated funnels*, according to the number of the testes, leading into efferent ducts. All the four ducts, when four are present, may remain distinct, or the two ducts of each side may open into a common atrium, or they may unite to form a common elongated *vas deferens*, opening at the male genital aperture. In connection with the terminal part of each vas deferens in many Oligochæta is a gland known as the *prostate* or *spermiducal gland*. Near the aperture of the vas deferens in many Earthworms are special setæ, the *penial setæ*.

There are never more than two *ovaries*, which, like the testes, are of very small size. The ova may become mature in the ovary, or groups of cell may be detached from the latter and one cell in each group ripen into an ovum. A *receptaculum ovorum* occasionally receives the ova after they leave the ovary. There are two *oviducts*, which open by funnel-shaped apertures into the cœlome. *Receptacula seminis* are present.

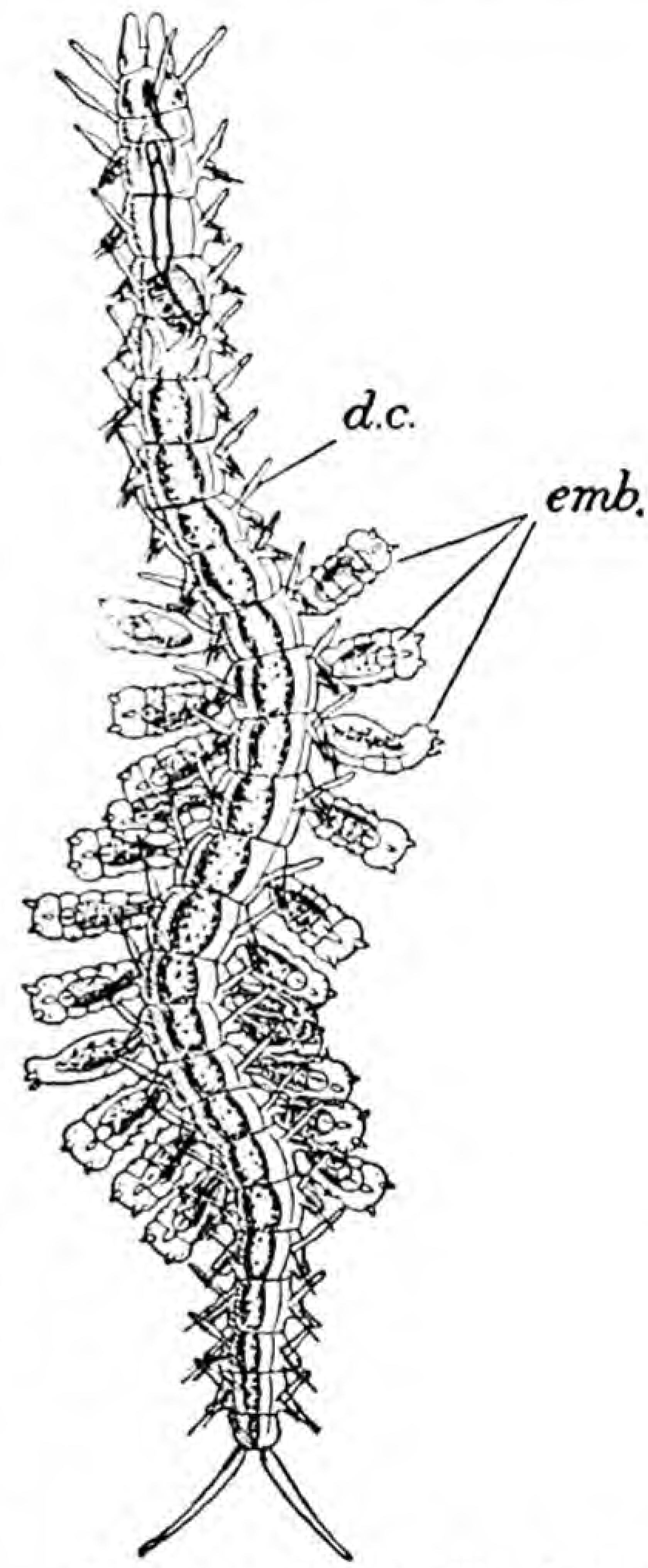


FIG. 309.—**Pionosyllis elegans.** Dorsal view of female with advanced embryos attached to the ventral surface. *d. c.* dorsal cirri; *emb.* embryos. (From Potts, after Pierantoni.)

Development.—The Oligochæta deposit the eggs in *cocoons*, either buried in the earth or attached to water-plants. The cocoon contains, in addition to a number of fertilized ova, a quantity of an albuminous fluid which serves as nourishment to the developing embryos. Cleavage is always unequal. In the forms in which food-yolk is scanty there is a process of embolic invagination (*Lumbricus rubellus*); in the others (*Tubifex*, etc.) the process is of the epibolic type. In the former case a blastula and an invaginate gastrula are formed in the way already described in the case of the Earthworm. In *Lumbricus trapezoides* the gastrula divides into two, each half subsequently giving rise to an embryo. The micromeres spread over the macromeres very much as in the Polychæta. A pair of mesoderm cells early appears, and by their division forms the mesoderm bands. No free larval stage similar to the trochophore occurs in any of the Oligochæta, but the stage intervening between the completion of the gastrula and the commencement of the segmentation of

the mesoderm bands corresponds to the trochophore in essential respects; and in some forms there is recognizable a feebly developed circlet of cilia comparable to the prototroch, and in some a pair of head-nephridia.

Fertilization and the development of the embryo take place externally in

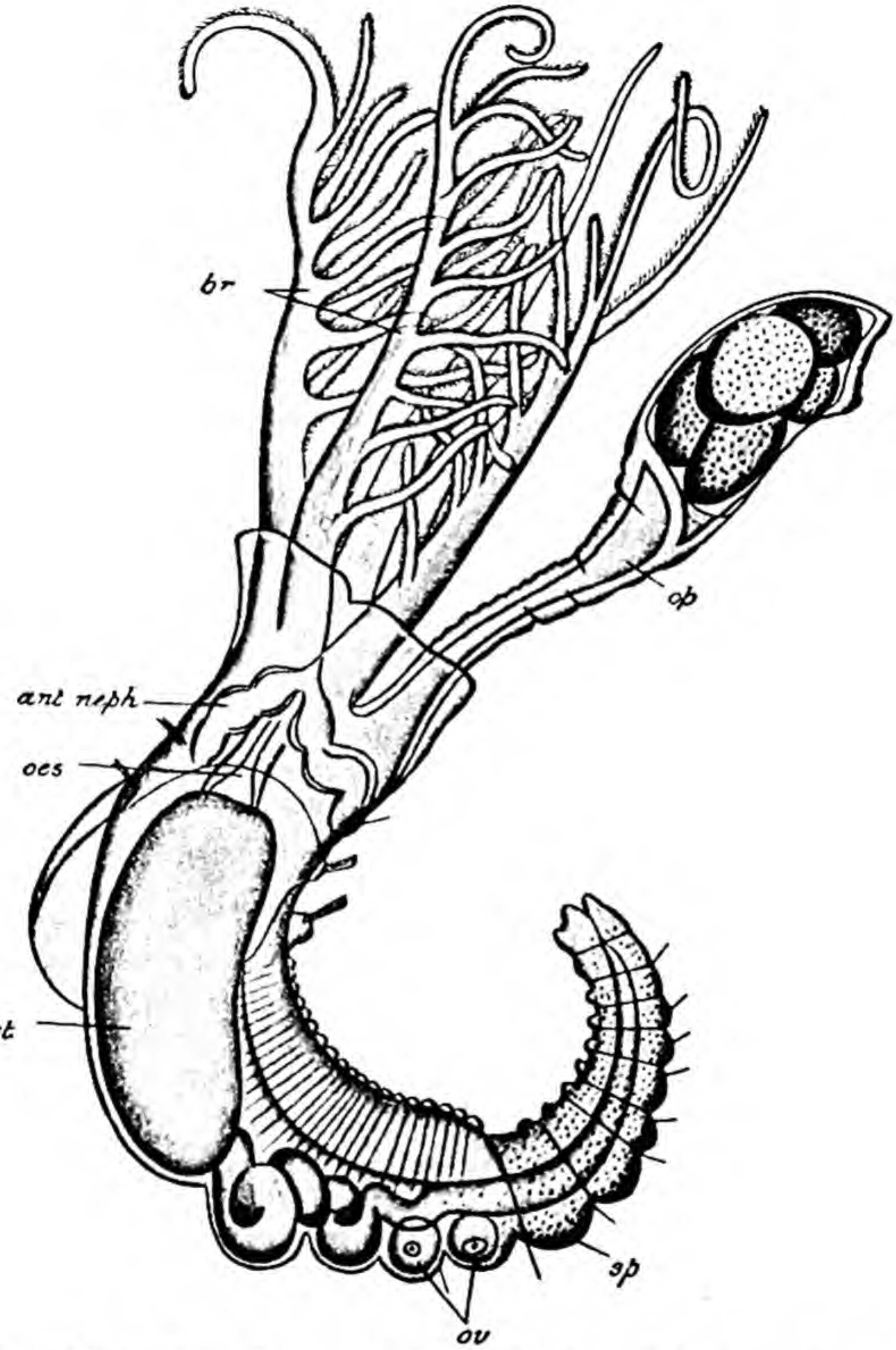


FIG. 310.—**Spirorbis lævis,** a hermaphrodite tubicolous Polychæt. Lateral view of entire animal. *ant. neph.* anterior nephridium; *br.* branchiæ; *œs.* œsophagus; *op.* operculum with developing embryos in its interior; *ov.* ova; *sp.* sperms; *st.* stomach. (After Claparède.)

all the Chætopoda, with a very few exceptions in which development occurs in the cœlome or in the interior of a dilated segmental organ. In the Polychæta, in the great majority of cases, fertilization takes place by the sperms coming in contact with the ova when both have become discharged, and the development

of the embryos goes on while they are floating freely in the sea. There are a few cases in which the fertilized ova are received into a sort of brood-pouch and there pass through at least the earlier stages of their development. Such a brood-pouch is formed in certain Errantia by the raising up of the integument on the ventral surface. In some species of Polynöe and allied genera, the fertilized ova and the resulting embryos adhere in masses to the dorsal surface under the shelter of the elytra; in some other Polychæta (certain Syllidæ) they are stuck by means of a viscid secretion to the dorsal or the ventral surface (Fig. 309), or to the cirri. In certain Sedentaria (Fig. 310) they develop in a cavity in the operculum; in others, in the interior of the tube, between the body of the worm and the inner surface of the latter, or on its outer surface. In some, again, though the ova do not remain in any way attached to the parent worm, they may be deposited in clumps or packets enclosed in gelatinous matter. Usually they have no other covering but the egg-membrane.

The cleavage of the ovum in the Polychæta is unequal. In the great majority the inequality between the macromeres and micromeres is very marked. In some Serpulids, however, the difference is very slight, and the two sets of cells are at first scarcely distinguishable. In such cases the cells arrange themselves in such a way as to form the wall of a hollow sphere, the *blastula*, with an internal closed cavity, the blastocœle. The macromeres, which may or may not have been distinct from the first, lie on one side of the blastula; and soon this side becomes invaginated (Fig. 311, *A*), the result being the formation of an *embolic gastrula*. In the great majority of forms, however, an *epibolic gastrula* is formed after the manner already described in the case of Nereis; but forms of the process of gastrulation intermediate between these two extremes have been observed. The blastopore of the gastrula, however formed, does not usually give rise directly either to the mouth or to the anus. It becomes elongated into a slit which becomes closed up, and the anus and proctodæum are formed by a fresh invagination in the original position of its posterior end, while another invagination of the ectoderm further forwards gives rise to the mouth and stomodæum. The embryo then passes into the *trochophore* stage.

The arrangement of the cilia on the surface of the trochophore varies in different Polychæta. Sometimes, though rarely, the pre-oral circlet is absent and the surface is covered uniformly with cilia in addition to an apical tuft: such larvæ are said to be *atrochal*. Typically there are two circlets close together, the one *pre-oral*, immediately in front of the mouth, and the other *post-oral*, immediately behind it. Sometimes, in addition to the pre-oral circlet, there is a *peri-anal circlet* round the anal end (*telotrochal* larvæ). In some cases the pre-oral circlet is absent and the post-oral is situated about the middle of the body (*mesotrochal*), or there may be several between the mouth and the anal end (*polytrochal*).

The post-oral portion of the larva elongates, and traces of segmentation become visible; sometimes a series of constrictions is developed before there is any trace of parapodia, sometimes rudiments of the latter with their setæ are developed first. The number of segments, at first very small, becomes added to from behind as the body gradually elongates. The establishment of external segmentation is accompanied by the division of the mesoderm bands into a series of segments, the history of which has been sketched in describing the development of Nereis. The ectoderm of the ventral plate develops a median thickening which gives rise to the ventral nerve-cord. Anteriorly this becomes connected by a pair of thickenings at the sides of the mouth—the rudiments of the œsophageal connectives—with the developing cerebral ganglion.

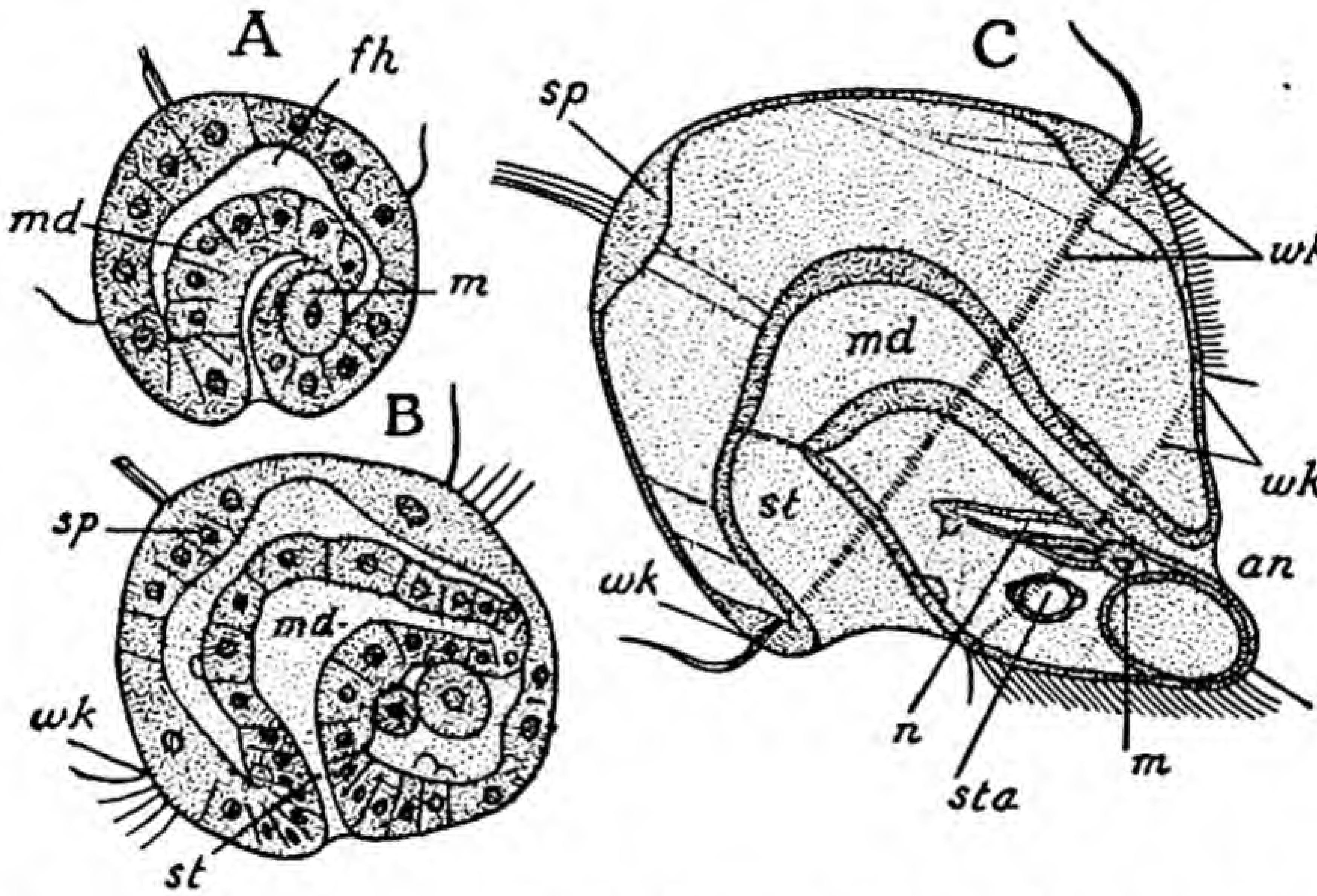


FIG. 311.—*A*, *B*, *C*, three stages in the development of the trochophore of **Eupomatus** (Sedentaria), from the side. *an*. anus; *fh*. blastocœle; *m*. polar cells of the mesoderm; *md*. mid-gut; *n*. larval head-nephridium; *sp*. neural plate; *st*. stomodæum; *sta*. statolith; *wk*, pre-oral ciliated ring; wk_1, post-oral ciliated ring. (From Lang's *Comparative Anatomy*, after Hatschek.)

The completion of metamorphosis is brought about by the increase in length of the body and concomitant increase in the number of segments, by the full development of the various systems of internal organs, and by the formation of the tentacles and other appendages. The parapodia, when first formed, very usually bear relatively long *provisional setæ*, which are subsequently thrown off to make way for those of the adult.

Asexual reproduction by simple fission followed by regeneration of the lost segments, or by proliferation followed by fission, occurs in certain groups of Chætopoda both among the Oligochæta and the Polychæta. Simple fission occurs in *Salmacina*, one of the Serpulids: a constriction becomes formed at a certain point towards the posterior end, rudiments of a new set of cephalic

branchiæ bud out on one side at this point, and this posterior part becomes a distinct zooid, which is eventually separated off and develops the full number of segments characteristic of the adult. This is not in any way a case of alternation of generations, as both parent and offspring are similar and sexual (hermaphrodite). In *Nais* and *Chætogaster* (Oligochæta) there is multiplication by proliferation of the segments at the posterior end; then the appearance of a constriction separating off five or six of the most posterior segments followed by a fresh proliferation in front of the constriction; and then a second constriction appears five or six segments further forwards—the result being the development of a chain of zooids which remain for a time connected together. The sexual cells become fully developed only after the zooids have separated from one another.

In some of the Syllidæ there is a distinct *alternation of generations*. The asexual worm developed from the ovum gives rise by a process of posterior proliferation and constriction (Fig. 312) to sexual zooids, a number of which may remain for a time connected together in a string before undergoing separation. These sexual zooids become developed into

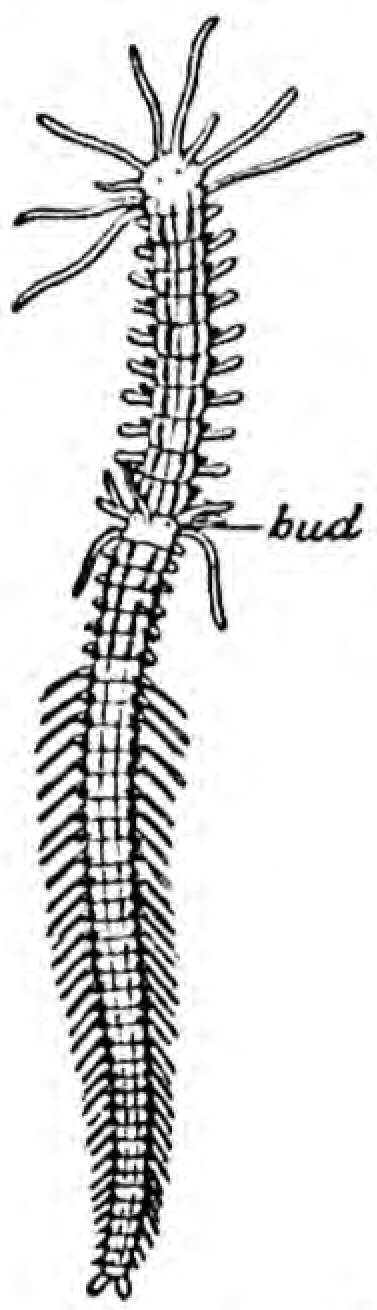


FIG. 312.—Budding in one of the **Syllidæ** (*Autolytus cornutus*); parent stock with a male zooid (*bud*) nearly ready to become detached. (After Agassiz.)

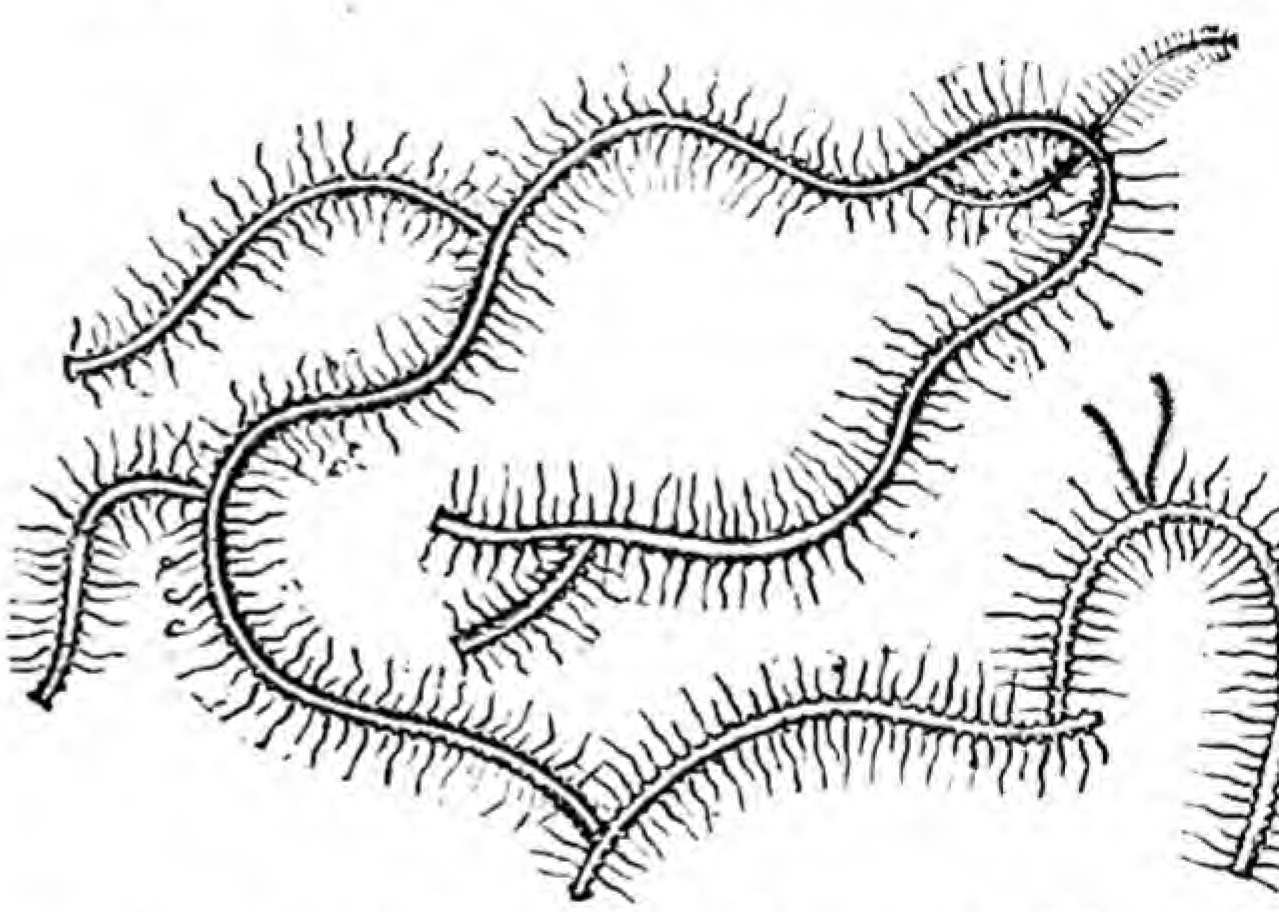


FIG. 313.—Portion of **Syllis ramosa.** (From the *Cambridge Natural History*, after McIntosh.)

mature males or females, which may be remarkably unlike the parent form in the shape of the parapodia, the character of the setæ, and other points; and in some instances the two sexes not only differ from the asexual parent form but also from one another, so that the three forms, before their relationship was known, were set down as representing three distinct genera.

Syllis ramosa (Fig. 313), which occurs in the interior of certain deep-sea sponges, is exceptional among the Chætopoda in giving rise by lateral branching to a colony from which sexual zooids afterwards become separated off.

Modes of Life, etc.—Very few Chætopoda are true *parasites*; but a considerable number are to be set down as *commensals*, habitually associating with

another animal for the sake of food and shelter. *Histriobdella* lives in the gill cavities and on the eggs of the European lobster and the Norway lobster, and *Stratiodrilus* (Fig. 314) in the gill cavities of Australian and Tasmanian fresh-water crayfishes. The Earthworms burrow in soil containing decaying vegetable matter, passing the mould through their intestine and subsequently throwing it out in the shape of castings on the surface. They also feed on decaying leaves, and sometimes on animal substances. Some of the freshwater Oligochæta (*Tubificidæ*) manufacture tubes of mud held together by a tenacious secretion from the epidermal unicellular glands. Some of the Errantia form temporary tubes of a gelatinous character, or more permanent parchment-like tubes sometimes strengthened by means of agglutinated sand-grains. But

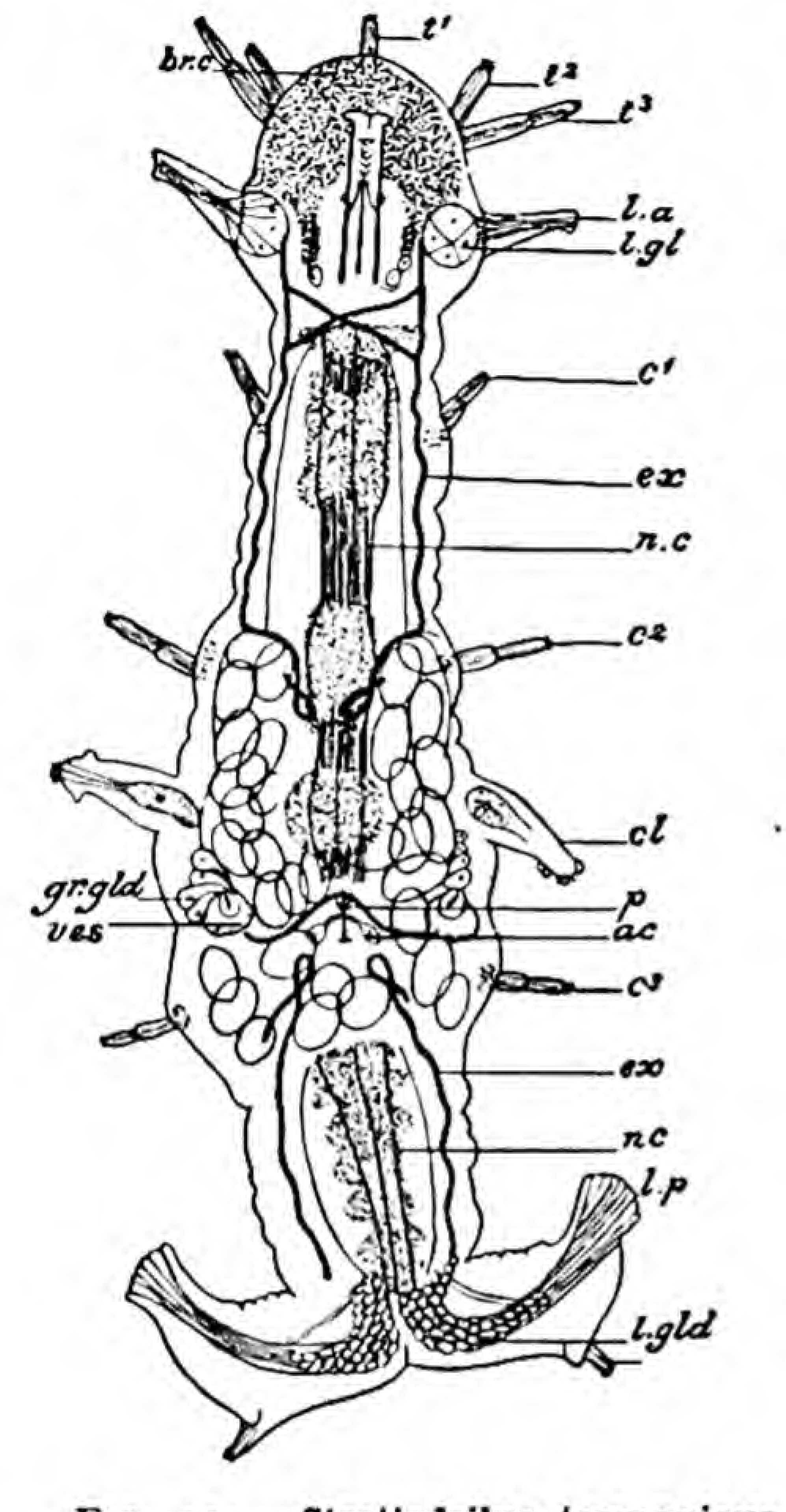


FIG. 314.—**Stratiodrilus tasmanicus,** male. *ac.* accessory gland of male apparatus; *br. c.* brain; c^1. c^2. c^3. cirri; *cl.* claspers (appendages peculiar to the male); *ex.* excretory tubes; *gr. gld.* granule-gland; *l. a.* anterior limb; *l. gl.* gland at base of anterior limb; *l. gld.* gland at base of posterior limb; *l. p.* posterior limb; *n. c.* nerve-cord; *p.* penis; t^1. t^2. t^3. tentacles; *ves.* vesicula seminalis.

FIG. 315.—**Serpulæ** with their tubes. (After Quatrefages.)

the majority of the Errantia, which for the most part prey on other small animals, are not confined to tubes, but move about freely. Some burrow in sand; others even in harder substances, such as the shells of Mollusca, or in limestone, shale, or sandstone. Many Sedentaria secrete tubes the substance of which is derived from the epidermal glands. These tubes are some-

times membranous or parchment-like, sometimes membranous but hardened by the deposition of grains of sand or particles of broken shells or bits of sea-weed; sometimes as in *Serpula* (Fig. 315) and *Pomatoceros* they are of a hard, shelly, calcareous character, sometimes composed entirely of foreign particles cemented together; very frequently they are permanently fixed to foreign objects. Some, such as species of *Polydora* and *Trophonia* (*Stylarioides*), near relatives of which construct tubes, excavate galleries in rock or coral or in the shells of various Mollusca.

A few Polychæta, such as the *Alciopidæ* and *Tomopteris*, as well as, in a certain phase, the *Nereidæ* and *Syllidæ*, are pelagic; but the majority live on the sea-bottom. They occur in the greatest abundance near the shore; but are also found at all depths in the ocean, the tube-dwelling forms being more abundant than the free forms in the deeper zones.

Owing to the soft character of most of their parts, there are comparatively few actual remains of Chætopoda in the older geological formations, though there are many burrows and tracks which have been ascribed to members of that class. Tubes of tubicolous Polychæta have, however, been found in formations dating from the Cambrian period onwards. Some tubes, not distinguishable from those of the existing genus *Spirorbis*, are found as far back as the Silurian; and others, apparently closely related to the living Serpula, as far back as the Carboniferous. In addition there are a number of tubes of extinct forms ascribed to the tubicolous Polychæta. The horny jaws of various Polychæta have been detected in strata from the Cambrian period onwards; and many tracks and burrows occurring in rocks of all ages are ascribed, some with more, some with less certainty, to this group of worms. No fossil remains of Oligochæta are known.

APPENDIX TO THE CHÆTOPODA.

THE MYZOSTOMIDÆ.

The *Myzostomidæ* are a group of worms which are now generally included among the Errantia, though possessing certain special features of their own. They are all external, or, in one case, internal, parasites of various Crinoids—both of the stalked and the free varieties, or internal parasites of certain Starfishes. They are disc-shaped animals (Fig. 316) (elongated in *Stelechopus*) devoid of any trace of external segmentation. There are patches of cilia here and there on both dorsal and ventral surfaces. At the sides there are five pairs of parapodia (*p*), each with a chitinous hook and a supporting rod; in the intervals between these there are in *Myzostoma* four pairs of small "suckers"; and round the margin is a series of ten or more pairs of cirri provided terminally with motionless sensory cilia, and with a ventral groove lined by adhesive cells. The mouth, usually situated at the anterior extremity, leads into a muscular pharynx (Fig. 317, *ph.*) capable of being protruded as a proboscis; from this a narrow œsophagus leads to the stomach which gives off a number of branched lateral diverticula (*da.*). A short cloaca (*klo.*) leading from the stomach opens on the exterior, in most cases at the posterior end of the body, sometimes on the dorsal surface. There is no distinct cœlome, the space between the alimentary canal and the body-wall being filled by connective-tissue (parenchyma), leaving only the cavities in which the sexual elements are lodged. Bundles of dorso-ventral muscular fibres form imperfect transverse septa, as in some Platyhelminthes.

There is no blood-vascular system, and specialized organs of respiration are likewise wanting. There is a single pair of nephridia with funnel-shaped internal apertures and with external openings either into the cloaca or on the surface. The nervous system comprises a large stellate ganglion situated ventrally, probably representing a number of fused ganglia, and giving off a number of nerves; and two nerve-rings, one round the œsophagus, the other round the pharynx, the two rings being connected together by a series of longitudinal nerves. The œsophageal ring presents a very obscure dorsal thickening, which is the only representative of a cerebral ganglion.

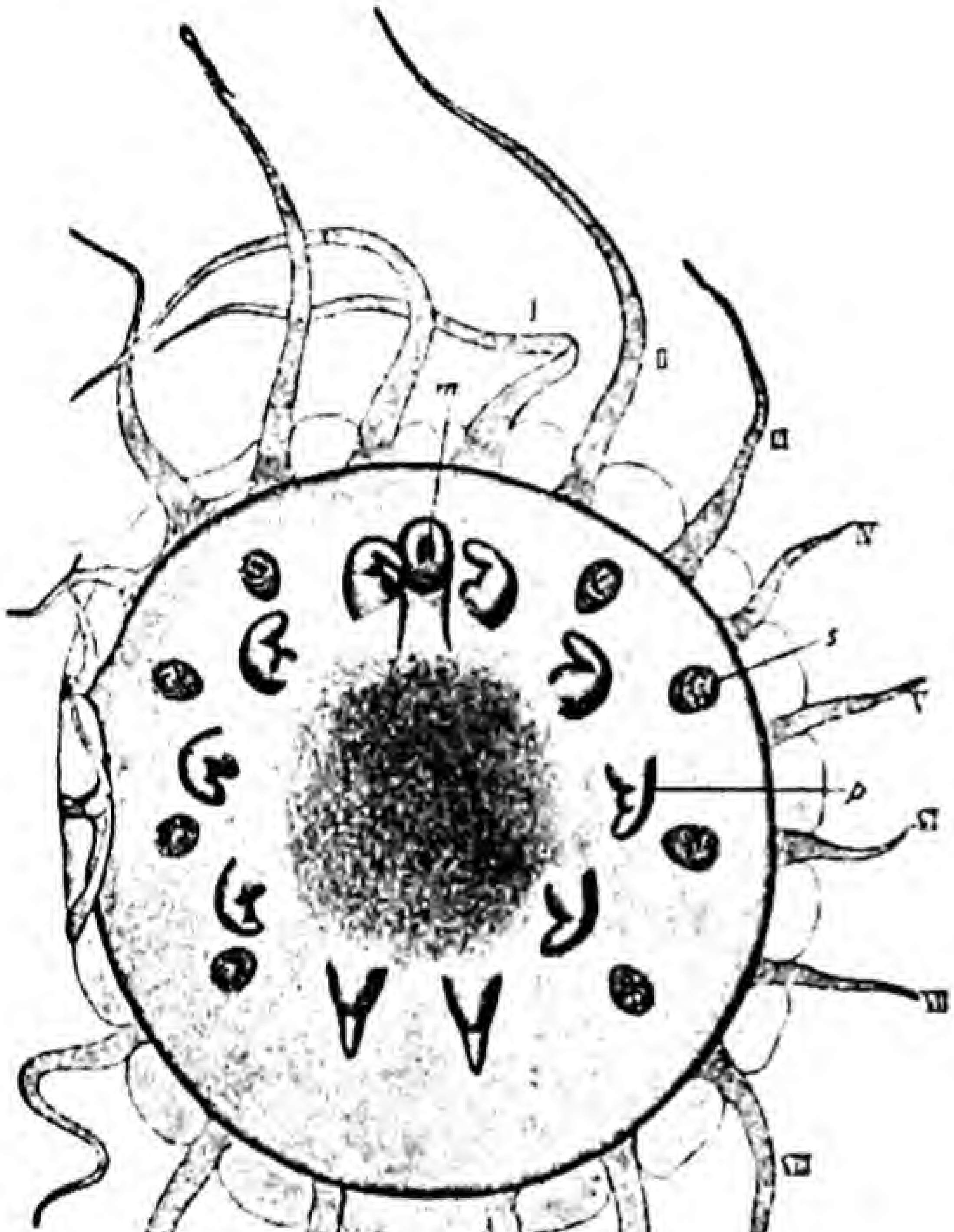


FIG. 316.—**Myzostoma.** I—X, cirri; *m.* mouth; *p.* parapodia; *s.* suckers. (After von Graff.)

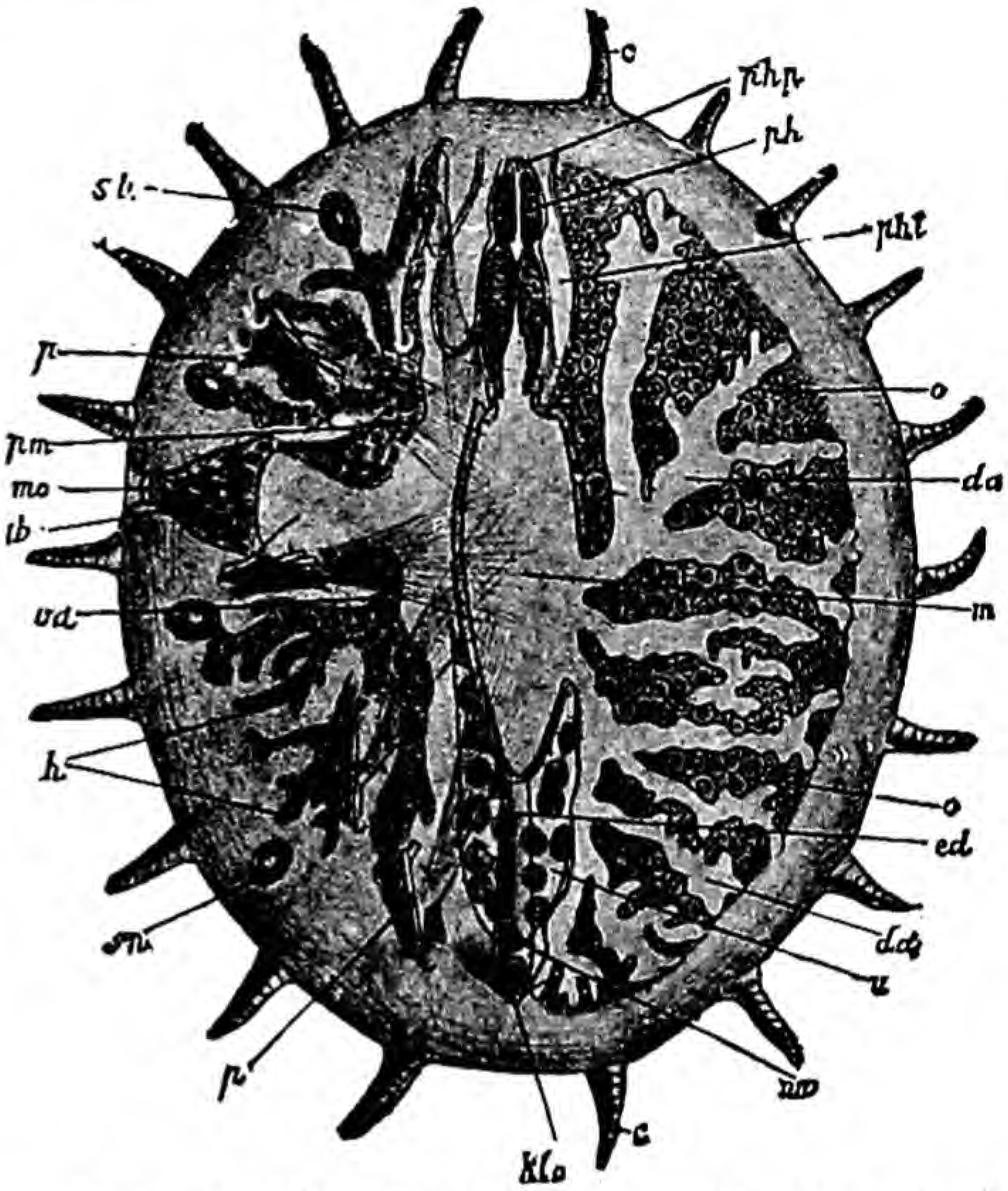


FIG. 317.—**Myzostoma.** Diagrammatic view of the internal organs. *c.* cirri; *da.* branches of the stomach; *ed.* hind-gut; *h.* testes; *klo.* aperture of cloaca; *m.* stomach; *mo.* male genital aperture; *o.* ovaries; *p.* parapodia, with hooks and supporting rod; *ph.* pharynx; *php.* pharyngeal tentacles; *pht.* pharyngeal pouch; *sb.* vesicula seminalis; *sn.* suckers; *u.* uterus; *wo.* female genital aperture. (From Lang's *Comparative Anatomy*, after von Graff.)

Most of the Myzostomidæ are hermaphrodite. There is a pair of ovaries formed by the proliferation of the layer of cœlomic epithelium covering the stomach; and in the sexually mature animal branching cœlomic spaces in the parenchyma, between the cæca, are found to be filled with ova (*o*). A posterior continuation of these spaces (*u*) opens either into the cloaca or independently of it. There are two elongated and usually branched testes (*h*), each of which has a vas deferens leading to a vesicula seminalis (*sb*) which opens near the lateral margin. In the hermaphrodite forms the testes are matured before the ovaries, and may have ceased to be functional before the ova become ripe.

The development of the Myzostomidæ closely resembles that of the Polychæta. A trochophore larva is first formed, and this becomes metamorphosed into a larva with provisional setæ bearing a close resemblance to that of Nereis.

CLASS II. HIRUDINEA.

1. Example of the Class—*The Medicinal Leech* (*Hirudo medicinalis* and *H.* (*Limnobdella*) *australis*).

The medicinal Leech is found in ponds, swamps, and slowly flowing streams in many parts of the world. *H. medicinalis* is the common British species: *H. australis* is an allied Australian form.

External Characters.—The Leech is a vermiform animal, some 6–10 cm. (2–3 inches) in length, but is capable of contracting and elongating itself so as to produce great alterations in form and proportions. It moves by "looping" movements, and is also a good swimmer. The body (Fig. 318) is depressed or flattened dorso-ventrally, the dorsal surface convex, the ventral flattened. The anterior end presents a ventrally directed cup-like hollow, the *anterior sucker* (*a. s.*), in the middle of which is a small aperture, the *mouth* (*mth.*). The hinder end bears a disc-like *posterior sucker* (*p. s.*), also directed downwards, and at its junction with the trunk, on the dorsal surface, is the very small median *anus* (*a.*). The animal is brightly coloured, the dorsal surface in *H. medicinalis* being longitudinally banded with alternate stripes of greenish-grey and rusty red, the ventral surface greenish-yellow, spotted with black: in *H. australis* the whole under-surface is rust-coloured.

The whole body is encircled by close-set transverse grooves, dividing it into *annuli*. These, like the annuli of some Earthworms, are more numerous than the true segments or metameres, the study of the internal organs showing that, except at the two extremities, each segment contains five annuli. There are also external characters by which the actual segmentation is plainly indicated. The rust-coloured streaks on the back of *H. medicinalis* are spotted with black, and at every fifth annulus the spots are larger than on the intervening rings: the annuli thus marked are the second of their respective segments. Moreover, the same rings bear on the ventral surface minute paired apertures, the *nephridiopores* or excretory apertures (*np. 1*, *np. 17*): of these there are altogether seventeen pairs, marking the first ring of the seventh and the second ring of the eighth to the twenty-third segments.

In front of the first and behind the last pair of nephridiopores one important external mark of segmentation fails, but a further indication is furnished by the presence on the middle ring of each undoubted metamere of a number of delicate transparent elevations, the *segmental papillæ* (*s.p.*), which have probably a sensory function. These structures are found along the whole length of the body, and as they mark the middle (third) ring of all those segments, the extent of which can be checked by the nephridiopores, it is legitimate to assume

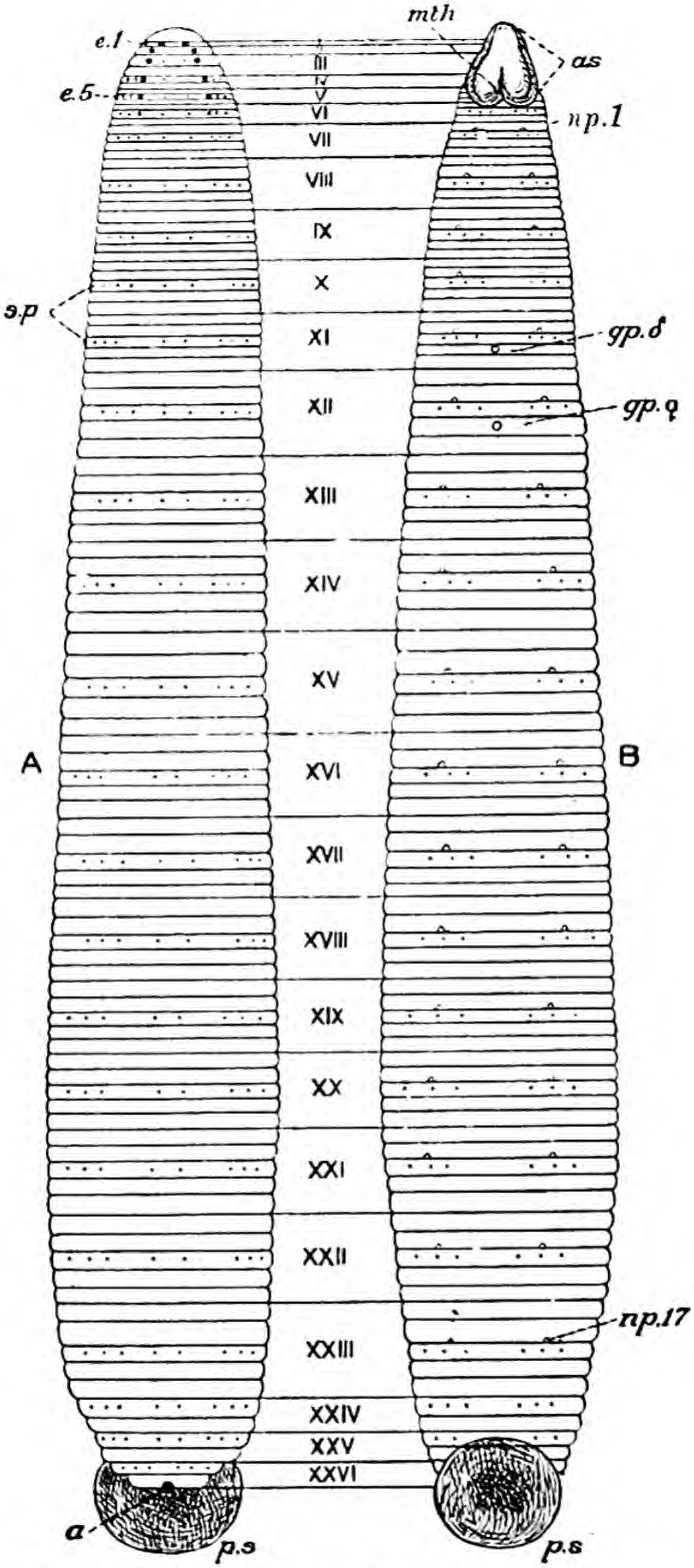


FIG. 318.—**Hirudo medicinalis.** *A*, dorsal; *B*, ventral aspect; *a.* anus; *a. s.* anterior sucker; *e. 1.* first, and *e. 5.* fifth pair of eyes; *g. p.* ♂. male gonopore; *g. p.* ♀. female gonopore; *mth.* mouth; *np. 1.* first, and *np. 17.* seventeenth pair of nephridiopores; *p. s.* posterior sucker; *s. p.* segmental papillæ; I.—XXVI. segments.

their segmental value in the anterior and posterior regions, where the controlling excretory apertures are absent. By the clue thus furnished it is found that there are six segments in front of that bearing the first pair of nephridiopores, and three behind that bearing the last pair, making a total of twenty-six metameres: of these the first seven and the last three have less than the normal number of rings.

The anterior sucker bears on its dorsal surface five pairs of small black spots, the *eyes* (*e. 1*, *e. 5*), the arrangement of which shows them to be special modifications of sensory papillæ, since they occupy in the first five segments the precise position occupied in the sixth and following segments by segmental papillæ.

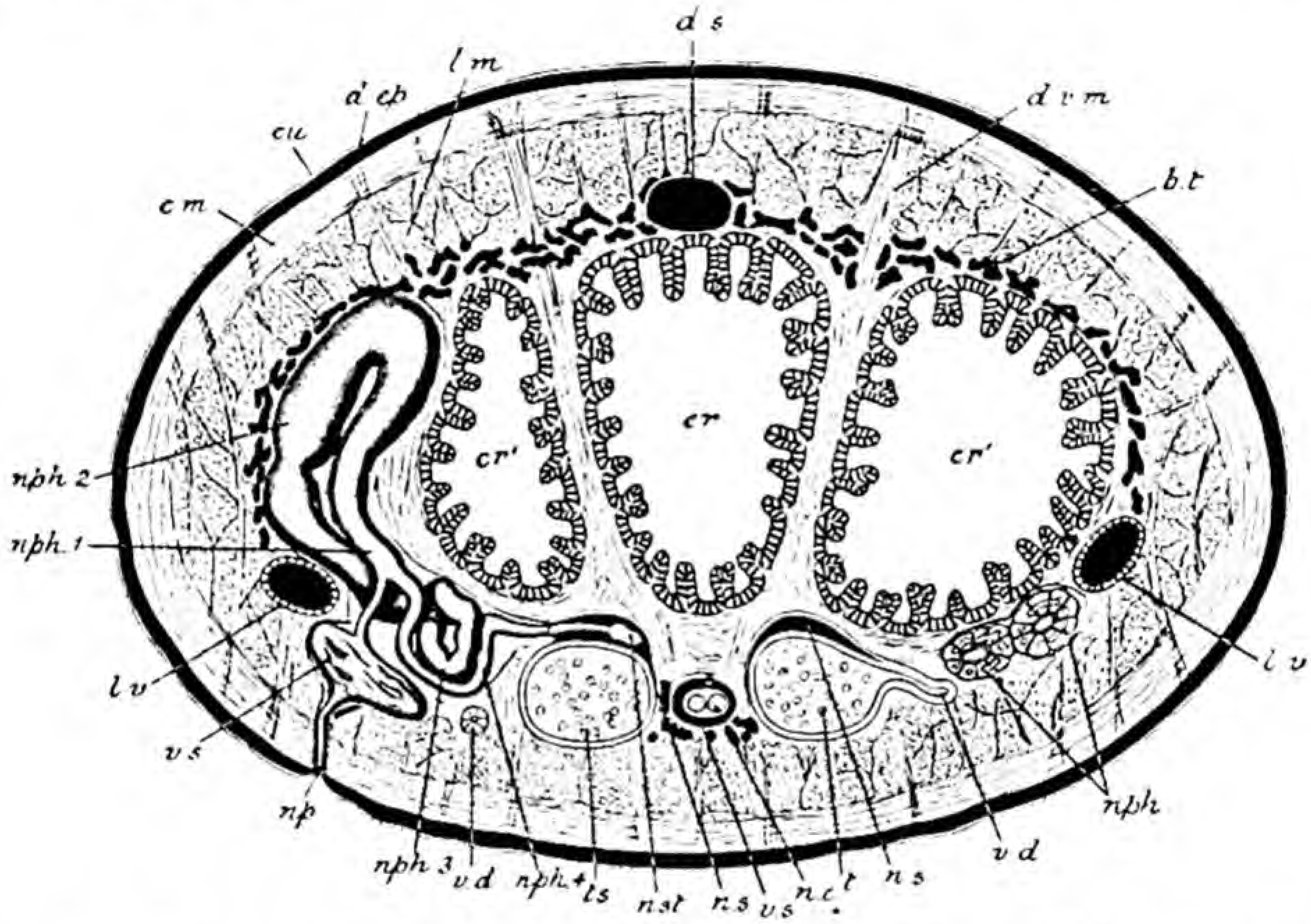


FIG. 319.—**Hirudo medicinalis;** transverse section. *b. t.* botryoidal tissue; *c. m.* circular muscles; *cr.* crop; *cr'.* diverticula of crop; *cu.* cuticle; *d. ep.* epidermis; *d. s.* dorsal sinus; *d. v. m.* dorso-ventral muscles; *l. m.* longitudinal muscles; *l. v.* lateral vessel; *n. c.* nerve-cord; *nph. 1–4*, nephridium; *n. s.* nephrostomial sinus; *nst.* ciliated funnel; *t. ts.* testis; *v. d.* vas deferens; *vs.* vesicle of nephridium; *v. s.* ventral sinus. (After Marshall and Hurst.)

The perfectly definite and comparatively small number of metameres in the leech offers a striking point of contrast with what we have met with in the Chætopoda, and is to be looked upon as a mark of higher differentiation.

Body-wall.—The body is covered externally by a thin cuticle (Fig. 319, *cu.*), which is constantly being cast off in patches and renewed. Beneath it is an epidermis (*d. ep.*) consisting of hammer-shaped cells, separated at their inner ends by spaces in which blood-capillaries run. The blood is thus brought into close relation with the surrounding water, and the skin becomes a highly efficient respiratory organ. The space between the epidermis and the enteric canal is filled by a peculiar form of connective-tissue, consisting of a gelatinous

matrix with interspersed cells and fibres, many of the former large and branched. More immediately surrounding the enteric canal and in close connection with the blood sinuses (*vide infra*) is the peculiar and characteristic *botryoidal tissue* (*b. t.*) consisting of large cells loaded with pigment. These cells recall the *chloragogenous cells* of the Chætopoda and have in all probability a similar *excretory* function.

Numerous unicellular glands are produced from the epidermis : the gland-cells themselves lie in the connective-tissue, and are continued into long ducts which open on the surface. Special glands in the ninth, tenth, and eleventh segments secrete the substance from which the cocoon is formed (*vide infra*, p. 363) : the segments in question therefore constitute the *clitellum*.

The **muscular system** is well developed, and consists of an outer layer of circular (*c. m.*) and an inner of longitudinal (*l. m.*) fibres. There are also dorso-ventral fibres (*d. v. m.*) passing vertically between the pouches of the crop (*vide infra*), and radial fibres extending from the wall of the enteric canal to the integument : these take the place of the septa of Chætopods.

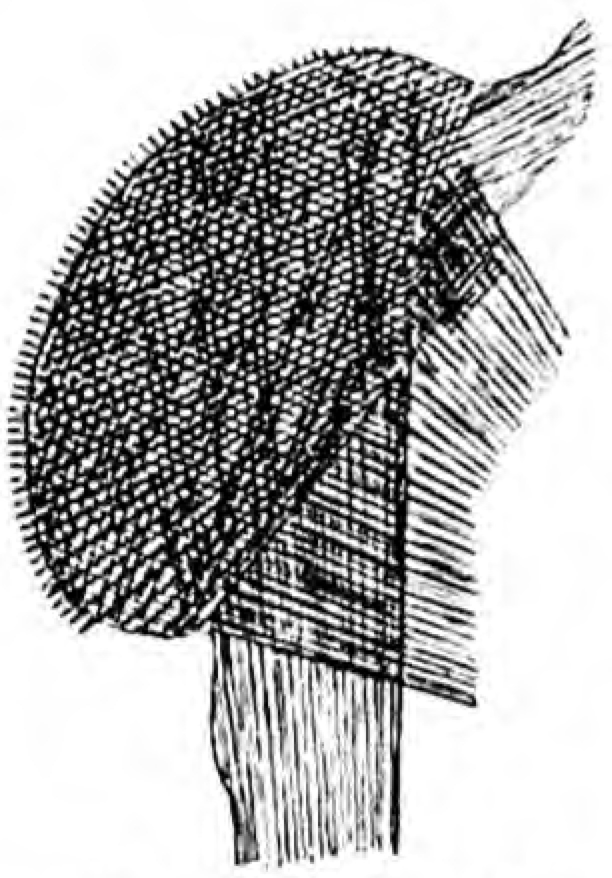


FIG. 320.—One of the jaws of **Hirudo medicinalis.** (After Leuckart.)

The **alimentary organs** are greatly modified in accordance with the bloodsucking habits of the animal. Surrounding the mouth are three *jaws*, one median and dorsal (Fig. 322, *d. j.*), the other two ventro-lateral (*v. l. j.*). Each (Fig. 320) has the form of a compressed muscular cushion, with a sharp, evenly curved, free edge covered with chitin, which is produced into numerous serrations or *teeth* : by means of its muscles each jaw can be moved backwards and forwards through a certain arc, and the three, acting together, produce the characteristic triradiate bite in the skin of the animal upon which the Leech preys.

The mouth leads into a muscular *pharynx* (Figs. 321 and 322, *ph.*) situated in the fourth to the eighth segments. Radiating muscles pass from its walls to the integument, and by their contraction dilate its cavity and suck in blood from the wounds made by the jaws. Around the pharynx are numerous unicellular *salivary glands*, which open close to the mouth : their secretion has the effect of preventing the coagulation of the blood taken as food.

The pharynx communicates by a very small aperture with the second and largest division of the enteric canal, the huge *crop* (*cr.*), a thin-walled tube extending from the eighth to the eighteenth segment and produced into eleven pairs of lateral pouches (*cr. 1*, *cr. 11*), the first ten of which are directed outwards and correspond each to a segment, while the eleventh (*cr. 11*) passes directly backwards as far as the twenty-fourth segment. The lumen is divided between the pairs of pouches by transverse septa, perforated by central apertures,

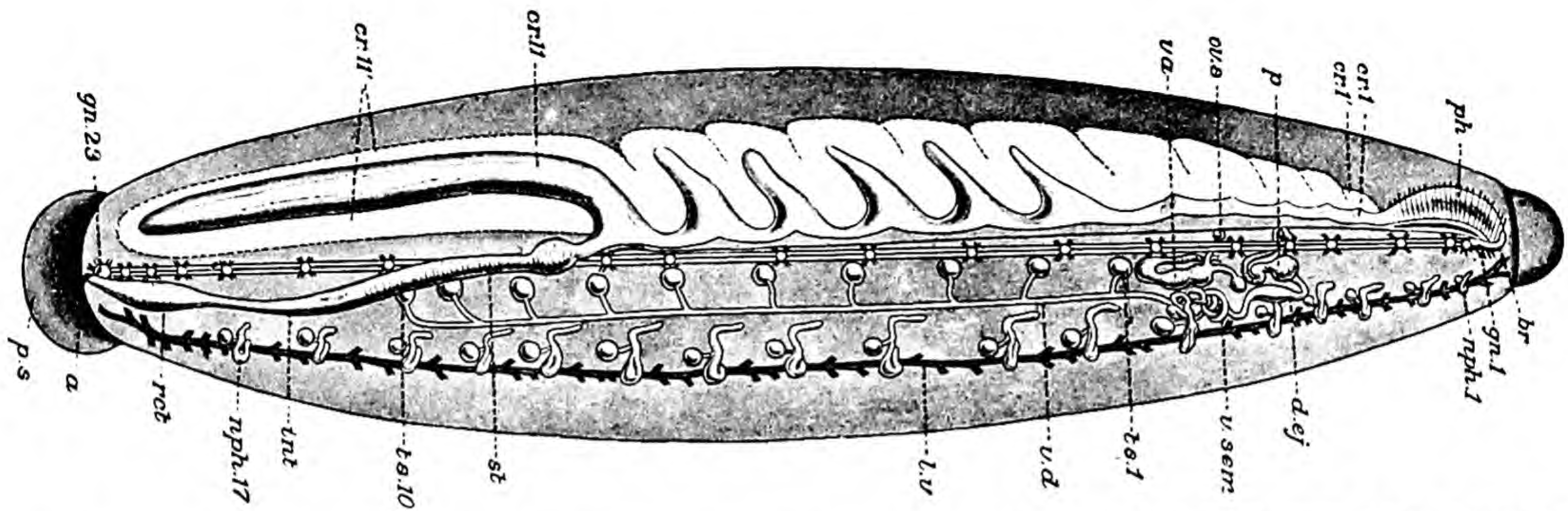


FIG. 321.—**Hirudo australis.** Dissection from the dorsal aspect; *a.* anus; *br.* brain; *cr. 1*, first diverticulum of crop, contracted; *cr. 1'*, the same expanded; *cr. 11*, the last diverticulum of the crop, contracted; *cr. 11'*, the same expanded; *d. ej.* ductus ejaculatorius; *gn. 1–23*, ganglia of ventral nerve-cord; *int.* intestine; *l. v.* lateral vessel; *nph. 1–17*, nephridia; *ov. s.* ovarian sac; *p.* penis; *ph.* pharynx; *p. s.* posterior sucker; *rct.* rectum; *st.* stomach; *ts. 1–10*, testes; *va.* vagina; *v. d.* vas deferens; *v. sem.* vesicula seminalis.

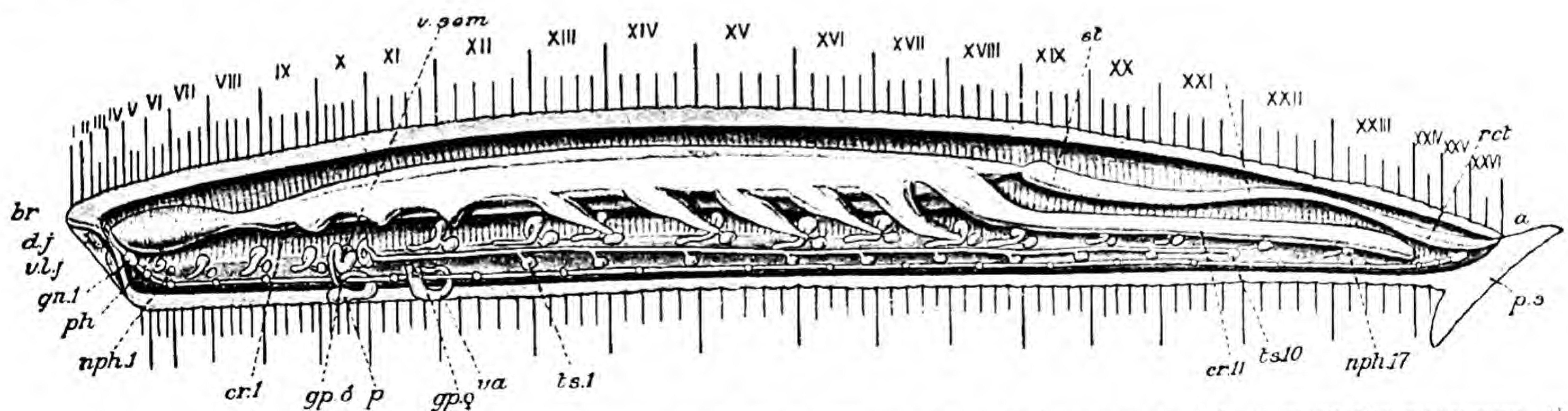


FIG. 322.—**Hirudo australis.**—Dissection from the left side, semi-diagrammatic; the longer vertical lines mark the metameres, the shorter lines the annuli. Lettering as in Fig. 321, and in addition *d. j.* dorsal jaw; *g. p.* ♂, male gonopore; *g. p.* ♀, female gonopore; *v. l. j.* ventro-lateral jaw.

into eleven chambers. The crop is capable of great dilatation, and its form varies greatly according to whether it is empty or gorged with blood. Posteriorly the crop communicates by a minute aperture with the *stomach* (*st.*), a tubular chamber with a dilated anterior end, and having its wall produced internally into a spiral fold: this is the digestive portion of the canal; the blood is passed into it from the crop with extreme slowness, and undergoes an immediate change, its colour turning from red to green. The digestion of a whole cropful of blood takes many months. The stomach is continued into a narrow *intestine* (*int.*): this passes into a somewhat dilated rectum (*rct.*) which turns slightly upwards and opens by the anus (*an.*) in the last annulus.

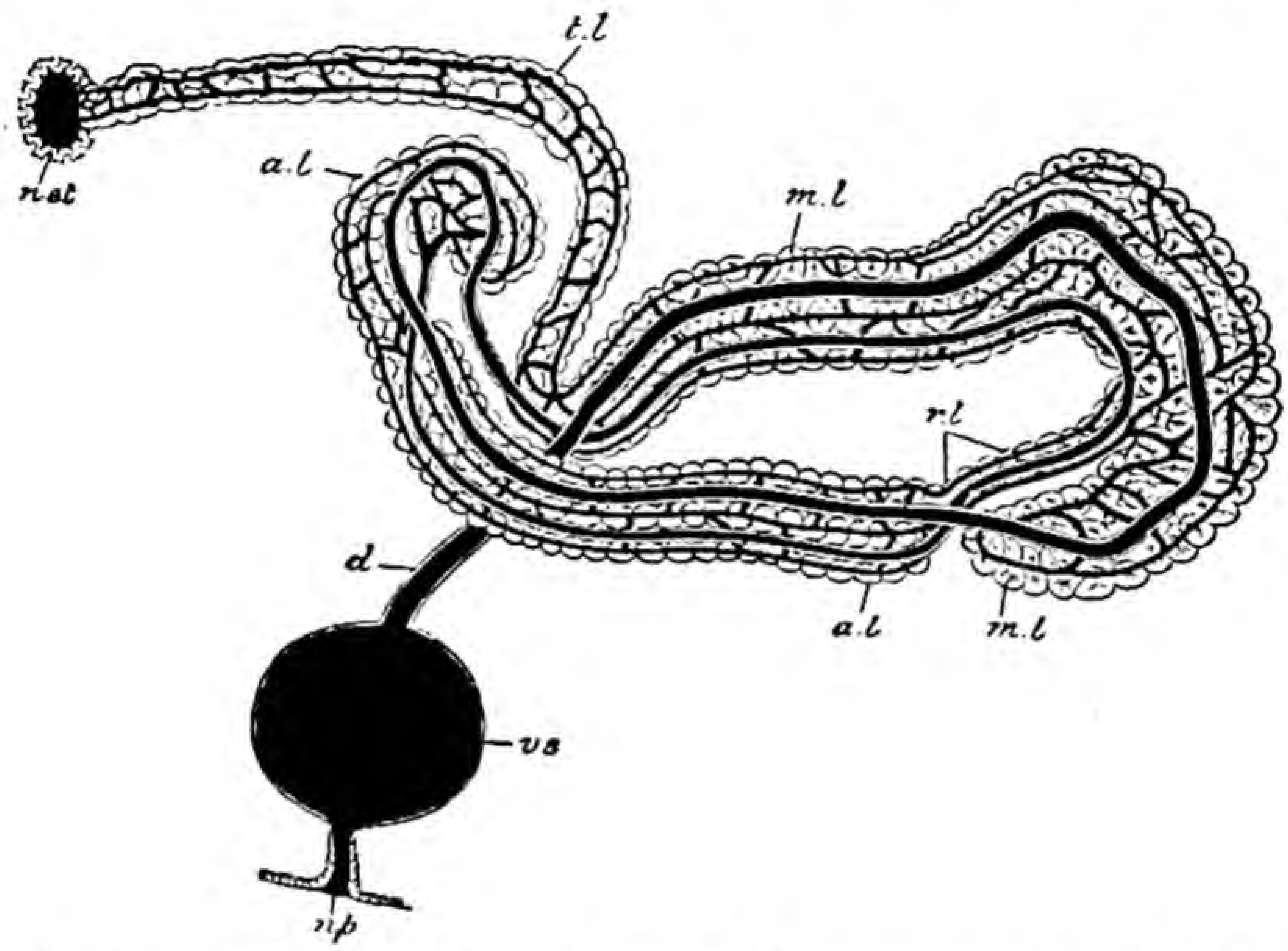


FIG. 323.—Nephridium of **Hirudo medicinalis.** *a. l.* apical lobe; *d.* vesicle-duct; *m. l.* middle lobe; *np.* nephridiopore; *nst.* ciliated funnel; *r. l.* recurrent lobe; *t. l.* testis-lobe; *vs.* vesicle. The communication here represented as existing between the ciliated funnel and the nephridial canals does not occur. (After Bourne.)

The **excretory system** consists of seventeen pairs of *nephridia* (*nph. 1–17*), situated in segments 7–23. A typical nephridium (Fig. 323) has the general form of a loop passing upwards from the ventral body-wall, produced into a free-ending offshoot which extends inwards towards the corresponding testis, and connected posteriorly with a small bladder or *vesicle* (*vs.*). The principal loop is divisible into two chief parts, the *main lobe* (*m. l.*) and the *apical lobe* (*a. l.*), connected with one another by a short *recurrent lobe* (*r. l.*): the free-ending offshoot towards the testis is called the *testis-lobe* (*t. l.*); it is abbreviated in *H. australis*.

All these parts are formed of a close-set mass of gland-cells, traversed by a complex system of minute intra-cellular passages or *ductules*, which finally unite into a comparatively wide inter-cellular tube or *duct*: this winds through

the main and apical lobes, and finally enters the vesicle, which opens posteriorly in the second annulus of the segment. The free end of the testis-lobe is swollen into a lobed mass (Fig. 319, *nst.*) which lies in a sinus in connection with the testis. This lobed body has a great number of small ciliated openings into the sinus in which it lies. In most of the nephridia (all except the first six pairs) modified ciliated funnels are present attached to the testis lobes of the nephridia, but these do not open into the canals of the latter.

There is a complex **blood-system** containing, like that of the Earthworm, red blood, the plasma coloured with hæmoglobin and containing sparsely distributed colourless corpuscles. But a striking difference from the preceding annulate types is found in the fact that the blood-containing spaces are of two

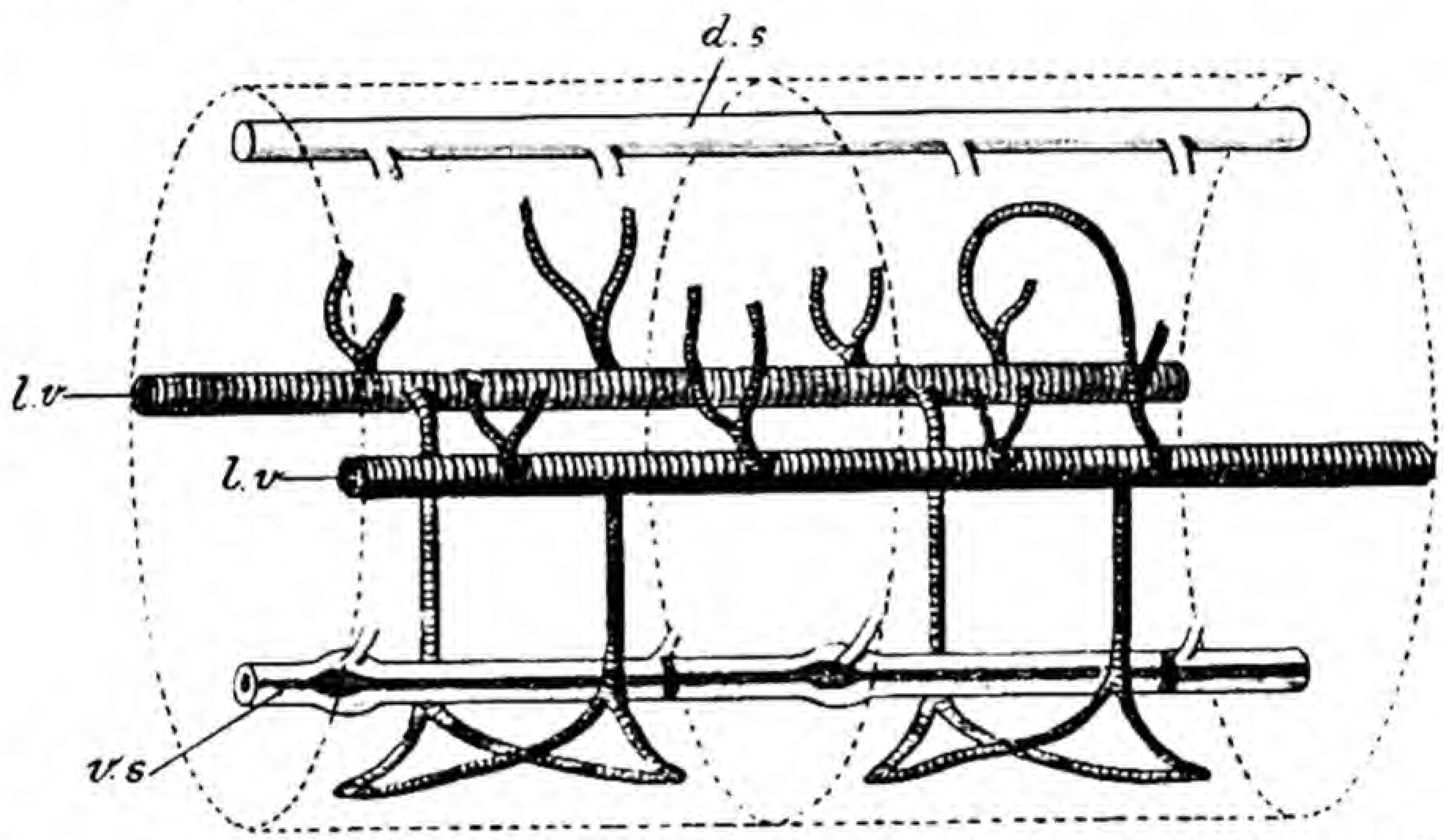


FIG. 324.—Diagram of principal blood-channels of **Leech.** *d. s.* dorsal sinus; *l. v.* lateral vessel; *v. s.* ventral sinus containing nerve-cord.

kinds—*blood-vessels* proper, having muscular walls; and *blood-sinuses*, the walls of which are devoid of muscle.

The two principal blood-vessels are lateral in position (Figs. 321 and 324, *l.v.*), running fore and aft at the level of the middle of the nephridia and uniting with one another at the anterior and posterior ends of the body. They send off branches both dorsally and ventrally, some of which anastomose with one another. The ultimate branches break up into capillaries in the integument, nephridia, etc.

The two principal sinuses are respectively dorsal (Figs. 319 and 324, *d. s.*) and ventral (*v. s.*), the former lying just above the enteric canal in the middle dorsal line, the latter occupying a similar position on the ventral side, and enclosing the ventral nerve-cord. The two sinuses are in connection with one another posteriorly, and are also in communication, by means of their branches, with the capillaries of the skin. There is thus the indirect connection, by means of capillaries, between the blood-vessels and the sinuses, but no direct com-

munication exists. The sinuses in which the ciliated funnels are lodged open into the ventral sinus. As we shall see more particularly in the general account of the class, the vessels and sinuses represent a greatly reduced cœlome.

The **nervous system** is of the usual annulate type. There is a small *brain* (Figs. 321 and 322, *br.*) situated above the anterior end of the pharynx immediately behind the median dorsal jaw. It is connected by a very short pair of œsophageal connectives with the ventral nerve-cord, which consists of twenty-three well-marked rounded ganglia (*gn. 1–23*), situated in the third or middle ring of each segment, united by delicate double connectives and a slender median strand. The ganglion-cells are regularly arranged in groups or packets. The first or sub-œsophageal ganglion is larger than the others, and is shown by development to be made up of five united pairs of embryonic ganglia: the last ganglion is also of unusual size, and results from the fusion of six pairs of ganglia distinct in the embryo. The whole ventral nerve-cord is contained in the ventral sinus. Nerves are given off from the ganglia, but not, as in the Earthworm, from the connectives, in which, also, nerve-cells are wholly absent.

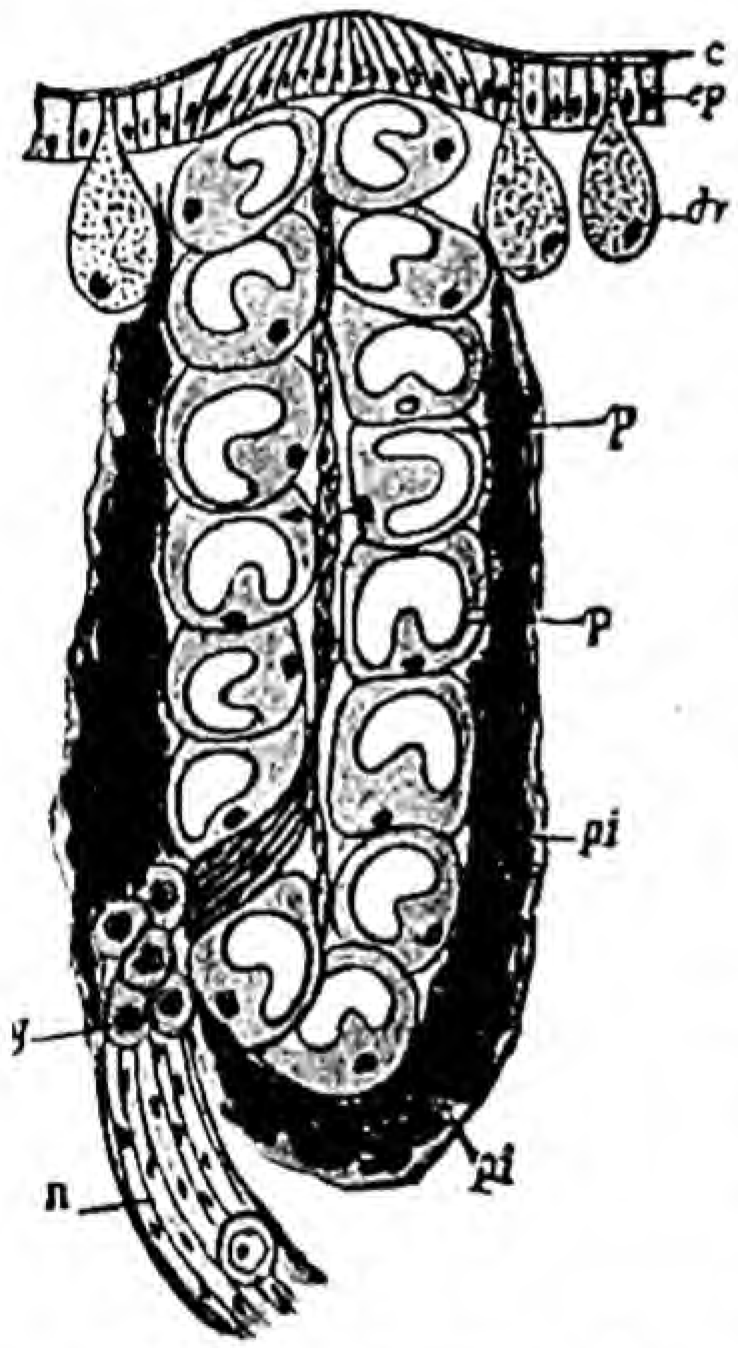


FIG. 325.—Section of eye of **Leech.** *c.* cuticle; *dr.* gland-cells; *ep.* epidermis; *g.* nerve-cells; *n.* nerve; *p.* refractive cells; *pi.* pigment. (From Lang's *Comparative Anatomy.*)

The principal **sense-organs** are the *eyes*, of which there are five pairs (Figs. 318 and 325) situated round the margin of the anterior sucker, on the dorsal side, one pair in each of the first five segments. They occupy positions taken in the succeeding segments by segmental sense-organs, with which they are obviously homologous. The structure of the eyes is peculiar: they are cylindrical in form (Fig. 325), the long axis of the cylinder being at right angles to the surface of the body. The outer layer is formed of black pigmented tissue (*pi.*), surrounding a layer of large, clear, refractive cells (*p.*), which occupy the greater part of the organ. A nerve (*n.*) enters at one side, and is continued up the axis of the cylinder by a row of sensory cells.

The margin of the anterior sucker also bears a large number of *goblet-shaped organs*, which are very probably organs of taste. The minute structure both of these and of the segmental sense-organs is very similar to that of the eyes. The function of the segmental sense-organs is unknown.

Reproductive Organs.—The Leech is hermaphrodite. There are nine or ten pairs of *testes* (Figs. 321 and 322, *ts.*), in the form of small spherical sacs, situated in segments 12 to 20 or 21. Each gives off from its outer surface a

narrow *efferent duct*, which opens into a common *vas deferens* (*v. d.*). In the tenth segment the vas deferens increases in width and forms a complex coil, the *vesicula seminalis* (*v. sem.*), from which is continued anteriorly a somewhat dilated muscular tube, the *ductus ejaculatorius* (*d. ej.*). From each ejaculatory duct a narrow tube passes to the base of the *penis* (*p.*), a curved eversible muscular organ which opens on the ventral surface of the fourth annulus of the eleventh segment, in the middle line. The base of the penis is surrounded by a number of unicellular glands, which constitute the *prostate*, and secrete a substance by which the sperms are aggregated into masses called *spermatophores*.

The *ovaries* are coiled filamentous bodies, each enclosed in a small globular *ovarian sac* (*ov. s.*), situated in the eleventh segment. From each ovarian sac a short *oviduct* passes inwards and backwards, and unites with its fellow into a median duct, the walls of which are supplied with albumen-secreting gland-cells. The common oviduct opens into a curved muscular tube, the *vagina* (*va.*), which opens in the middle line on the ventral surface of the fourth annulus of the twelfth segment, *i.e.*, one segment behind the male aperture.

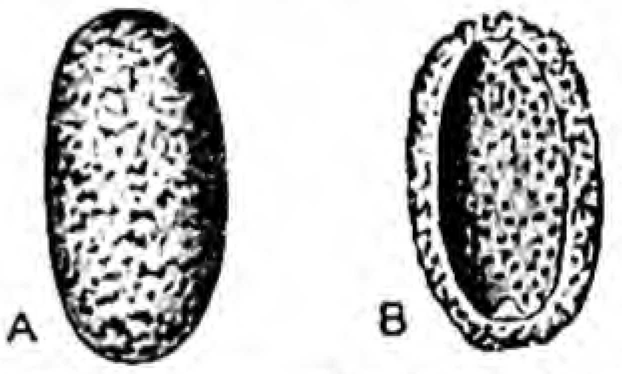


FIG. 326.—The cocoon of **Hirudo.** *A*, entire; *B*, in section. (After Leuckart.)

It will be noticed that the ovaries of the Leech form a single pair, while the testes are multiple and segmental: also that, while the gonads and efferent ducts of both sexes are paired, the penis and the vagina are median and unpaired. In the latter respect the contrast between the Leech and the Annelida previously discussed is very striking. Further important peculiarities are the enclosure of the ovary in a sac from which a duct leads directly to the exterior, and the fact that the testes are hollow sacs discharging the sperms into a cavity from which they pass directly to the efferent ducts. In Chætopods, it will be remembered, the gonads lie freely in the cœlome, and their products—ova or sperms—are discharged from their external surfaces and carried off either by cœlomoducts or by "segmental organs." It seems tolerably certain that in the Leech the cavities both of the ovarian sacs and of the testes represent shut-off portions of an almost obsolete cœlome, and that their ducts are cœlomoducts.

Development.—When breeding, two Leeches copulate, and one impregnates the other by passing spermatophores through its penis into the vagina. Simultaneous mutual impregnation has also been described. The clitellar segments (ninth to eleventh) secrete a cocoon (Fig. 326), into which spermatophores, ova, and a quantity of albumen, secreted by the gland-cells in the wall of the median oviduct, are passed. The animal then withdraws its head from the cocoon, the two ends of which close up by their own elasticity, producing a closed capsule in which embryonic development takes place. Cleavage is unequal, and results in the formation of a globular embryo, which, after

hatching, swims about in the cocoon, actively devouring its albuminous contents, and finally escaping in a form closely resembling the adult.

2. Distinctive Characters and Classification.

The Hirudinea are Annelida in which the body consists of a limited and definite number of segments, and is marked externally by secondary rings or annuli, a variable number of which go to a segment. The anterior end of the body is suctorial, and several of the hindmost segments are fused to form a powerful sucking-disc, which is directed downwards and backwards. The mouth lies in the anterior sucker, the anus is usually dorsal and immediately in front of the posterior sucker. The cœlome is always more or less obliterated by connective-tissue, and is represented by sinuses of varying dimensions which contain blood. True blood-vessels, with muscular walls, are also present. The nervous system consists of a brain united by short œsophageal connectives to a ganglionated ventral nerve-cord. The excretory organs are segmentally arranged nephridia. The sexes are united, the testes numerous and usually segmentally arranged, the ovaries a single pair. The testes have the form of sacs, and discharge their products internally: the ovaries either have a similar structure or are band-like and enclosed in ovarian sacs, into which the ova are set free. The penis and the vagina are unpaired, and open by median apertures, the male anterior to the female, on the ventral surface of the body. Development is usually direct, i.e. *unaccompanied by a metamorphosis. Leeches are either free-living, or are permanently or intermittently parasitic: they inhabit either the land, fresh-water, or the sea.*

The class is divided into the following orders:—

Order 1.—Acanthobdellida.

Hirudinea with short proboscis; without anterior sucker; closely related to the Oligochæta.

This order includes *Acanthobdella*, parasitic on Fishes.

Order 2.—Rhynchobdellida.

Hirudinea in which the anterior part of the body can be protruded and retracted so as to form a proboscis or introvert.

This order includes *Glossiphonia*, parasitic on Snails, Frogs, etc.; *Piscicola*, on fresh-water Fishes; *Pontobdella and Branchellion*, on marine Fishes (Fig. 327).

Order 3.—Gnathobdellida.

Hirudinea in which the mouth is provided with two or more, usually three, toothed jaws.

This order includes *Hirudo* (Fig. 318), the common Leech, parasitic on Vertebrata; *Aulostoma*, the Horse-leech, free-living and carnivorous; *Hæmadipsa*, the Land-leech.

ORDER 4.—HERPOBDELLIDA.

Hirudinea in which the mouth is not armed with true jaws.

This order includes *Herpobdella* (*Nephelis*), *Trocheta*, *Orobdella*, etc.—all fresh-water or terrestrial forms.

3. GENERAL ORGANIZATION.

In the essential features of their organization the Leeches are a very uniform group: there are, however, a few interesting modifications of structure which must be referred to.

Form and Size.—Most kinds do not exceed a few centimetres in length, but

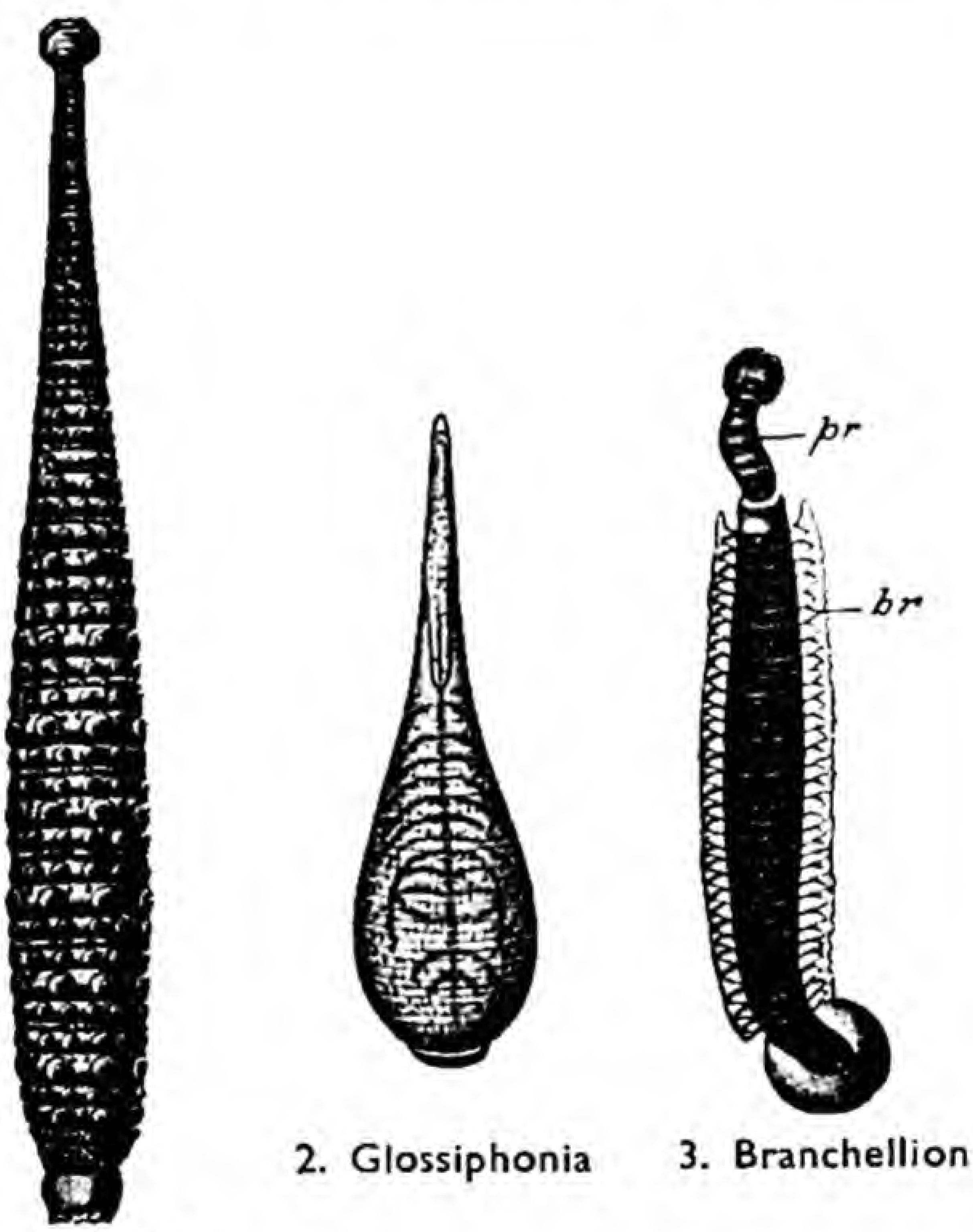


FIG. 327.—Three **Rhynchobdellida.** *br.* gills; *pr.* everted proboscis. (1, after Bourne; 2 and 3, after Cuvier.)

the American species *Cardea valdivania* is said to attain a length of 76 cm. ($2\frac{1}{2}$ feet). The number of annuli to a segment varies from two to fourteen and is constant in each species, but the general form of the body is remarkably uniform, the external differences between various species depending largely on colour and on the development of papillæ, which in some cases are large and prominent. **Setæ** are absent in all except one genus, *Acanthobdella*, which has two pairs on each side of the first five segments.

The **proboscis** (Fig. 328), the possession of which is distinctive of the Rhynchobdellida, is simply the retractile anterior end of the body, which, by the action of special muscles, can be drawn back into a temporary sheath. The organ is thus an *introvert*, like that of the Sipunculida (*vide infra*).

The chief differences in the structure of the **enteric canal** depend upon the varying number, or, in some cases, the total absence, of lateral pouches to the crop: for instance, the horse-leech has only a single pair, corresponding to the eleventh pair in Hirudo, while Herpobdella has none at all. In the Rhynchobdellida there is a distinct slender gullet (Fig. 328, *gul.*) leading from the pharynx to the crop (*cr.*), and thrown into a coil when the proboscis is retracted.

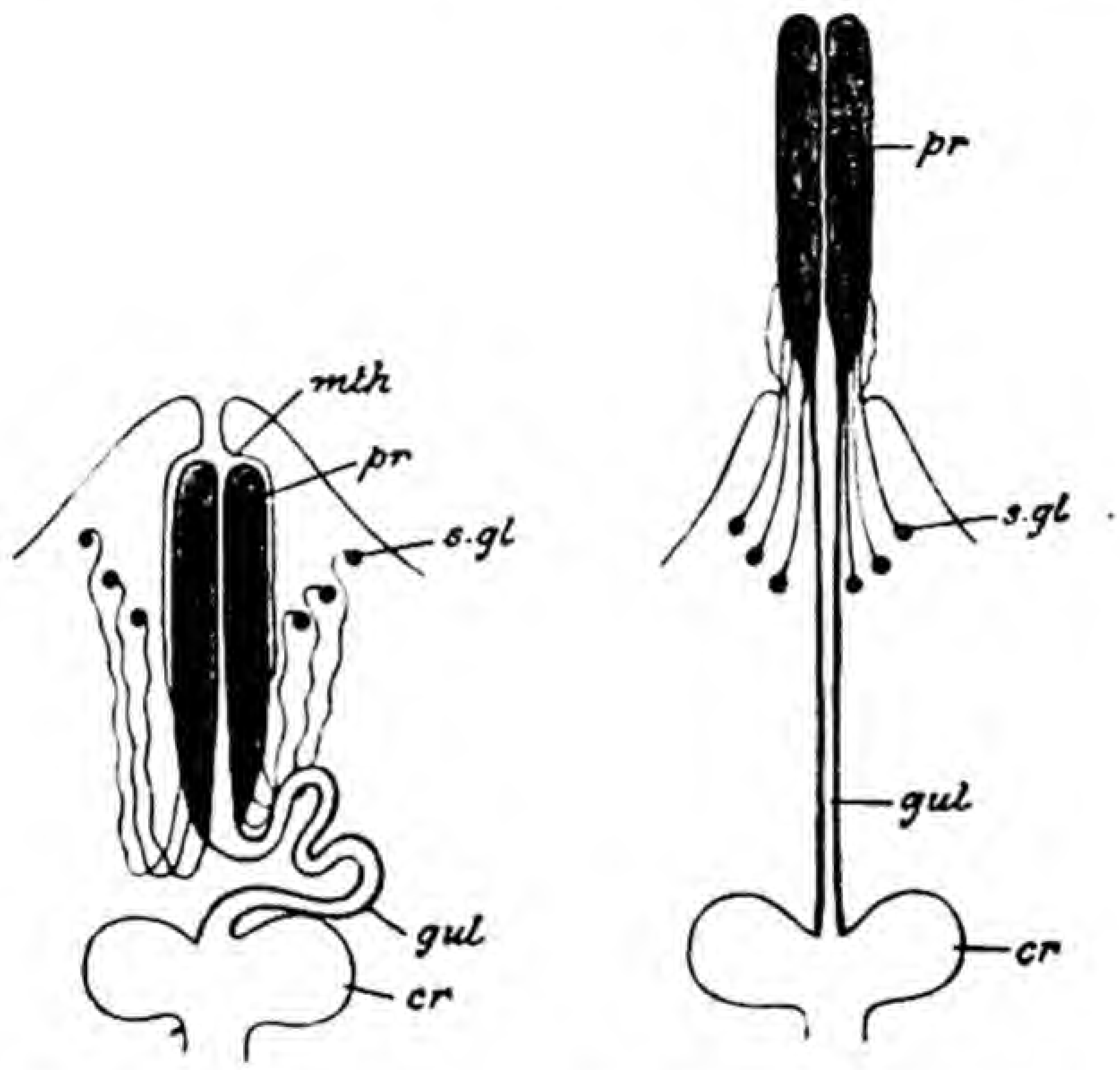


FIG. 328.—Proboscis of **Glossiphonia.** *A*, retracted; *B*, everted; *cr.* crop; *gul.* gullet; *mth.* mouth; *pr.* introvert; *s. gl.* salivary glands. (After Bourne.)

Among the Gnathobdellida the median jaw is absent in some land-leeches, and in other species all three jaws are rudimentary or absent.

Blood-system and **Cœlome.**—In the Medicinal Leech, as we have seen, there are lateral vessels with contractile muscular walls and dorsal and ventral sinuses with non-contractile walls. All of these seem to be formed, in this and the rest of the Gnathobdellida, from cœlomic spaces, and none of them, therefore, correspond developmentally to the true blood-vessels of the Chætopoda, which are formed independently of the cœlome. In the rest, however, the dorsal and ventral vessels are developed in the manner of true blood-vessels, while the lateral vessels or sinuses are always cœlomic in origin.

In *Pontobdella*, one of the Rhynchobdellida, there are dorsal and ventral as well as lateral vessels, and lateral as well as dorsal and ventral sinuses, and in each case the vessel is enclosed in the corresponding sinus. The ventral

sinus also contains the nerve-cord and the ovaries, and offshoots of it surround the testes and the nephrostomes. In the Rhynchobdellida in general the cœlomic spaces remain fairly extensive, and are lined by a cœlomic epithelium. Another interesting condition occurs in Herpobdella, in which the middle region of the body contains a series of paired, metamerically arranged spaces, surrounded by botryoidal tissue and containing the nephrostomes. Development shows that these cavities are derived from true cœlomic spaces in the embryo, formed, as in the Chætopoda, by a splitting of the mesoderm in each segment. *Acanthobdella*, already referred to as exceptional in the possession of setæ, is also the only member of the class which has a well-developed and spacious cœlome, divided by mesenteries into a number of segments.

In most instances the skin, with its abundant supply of capillaries, constitutes the only **respiratory organ**, but in *Branchellion* (Fig. 327, 3), a Rhynchobdellid parasitic on the Electric Rays (*Torpedo* and *Hypnos*), and on one of the Australasian Skates (*Raja nasuta*), differentiated respiratory organs or *gills* (*br.*) are present in the form of delicate lateral outgrowths of the segments.

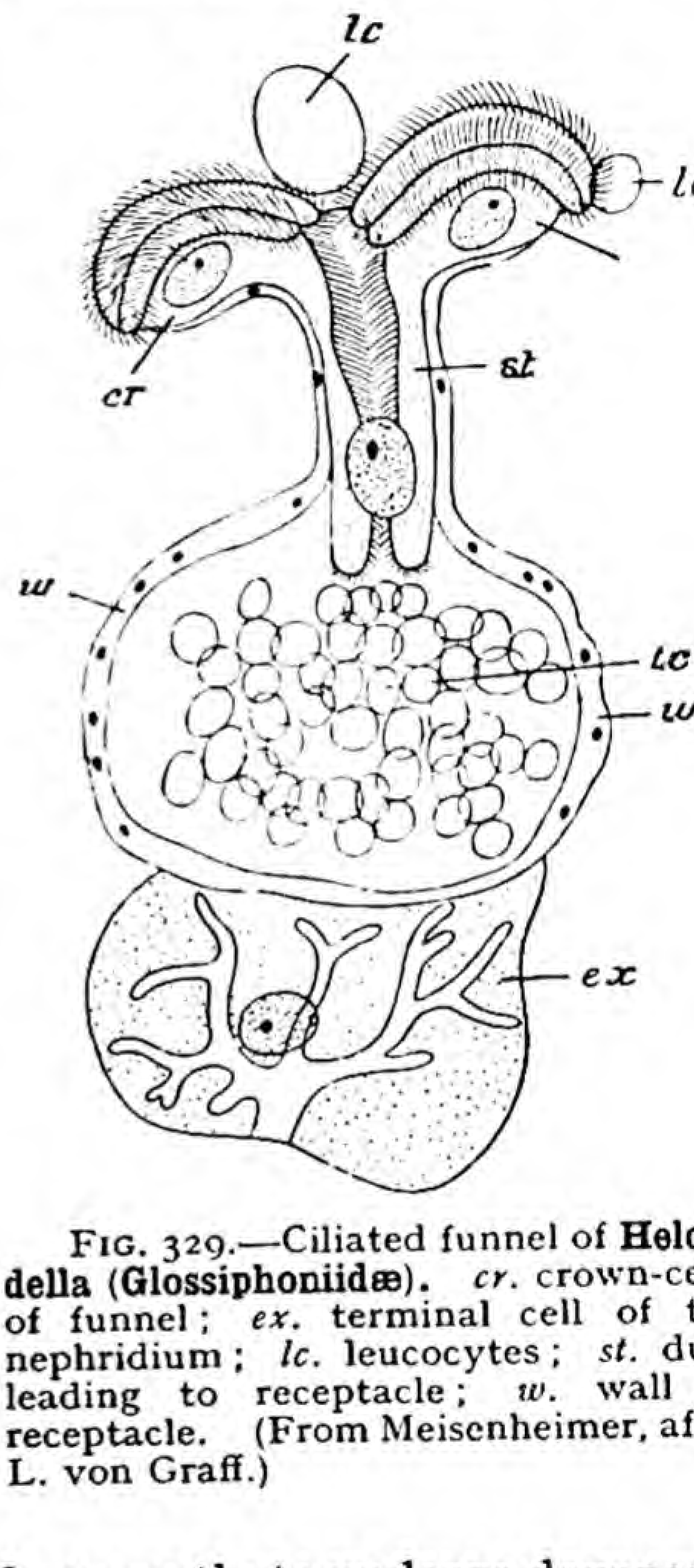


FIG. 329.—Ciliated funnel of **Helobdella (Glossiphoniidæ)**. *cr.* crown-cells of funnel; *ex.* terminal cell of the nephridium; *lc.* leucocytes; *st.* duct leading to receptacle; *w.* wall of receptacle. (From Meisenheimer, after L. von Graff.)

In most members of the class the **nephridia** are formed on the same general type as those of Hirudo, but differ in the structure of the ciliated funnels, which may be more or less modified, as in Hirudo. The funnels, where they occur, never open into the nephridial canals. Each funnel leads by a narrow ciliated duct into a *receptacle*, in which leucocytes laden with waste-matters are received from the cœlomic spaces and sinuses, subsequently to undergo degeneration and absorption (Fig. 329). By its outer side this receptacle is in close relation to the inner end of the nephridium, and the waste-matters from the disintegrated leucocytes are no doubt received into the nephridial canals and thus passed out to the exterior. The ciliated funnels of the Hirudinea correspond more closely with the cœlomoducts or ciliated organs of the Polychæta than with the nephrostomes; they are to be compared also with the "urns" of the Sipunculoidea. In the Rhynchobdellid *Pontobdella* a very interesting modification of the nephridial system occurs. Instead of distinct nephridia, there is

found on the ventral surface of the body a very complex network (Fig. 330, *nph.*), which sends off on each side of each segment a short branch terminating in a ciliated funnel, and a similar branch which opens externally (*np.*). A similar modification occurs in *Branchellion.*

The **nervous system** always closely resembles that of Hirudo, as also do the **sense-organs**. The number of eyes is subject to considerable variation: they may be developed on the posterior sucker, or may be absent altogether.

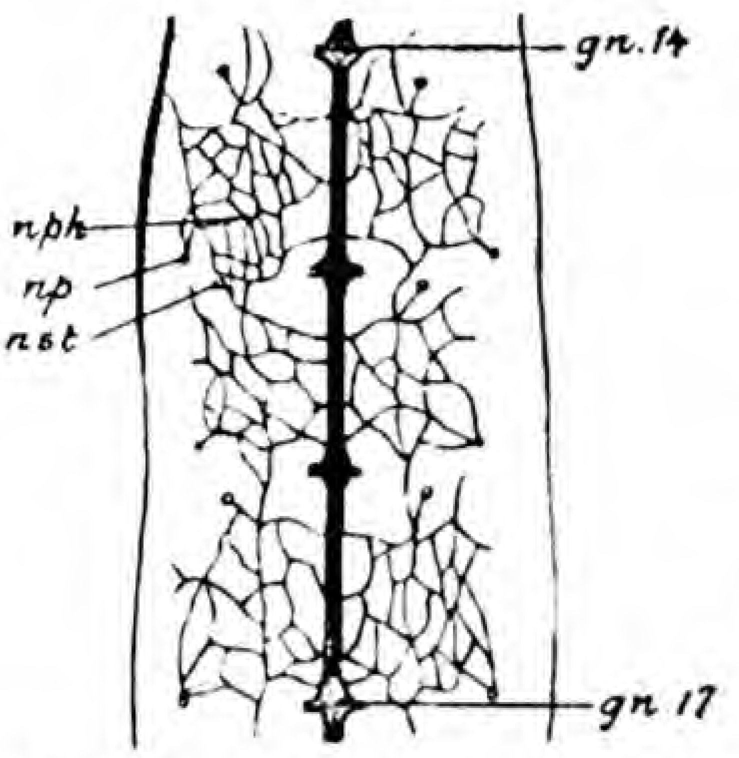


FIG. 330.—Nephridial system of **Pontobdella.** *gn.* 14, *gn.* 17, ganglia of nerve-cord; *np.* nephridiopore; *nph.* nephridial network; *nst.* ciliated funnel. (After Bourne.)

Reproductive Organs.—The *testes* usually have the segmental arrangement found in Hirudo, their number varying from five to twelve pairs. But in Herpobdella they are very numerous, and are not arranged segmentally. In the Rhynchobdellida the muscular penis is absent, its place being taken by an eversible sac. The form of the ovary with its containing sac in Hirudo is exceptional. As a rule, there is an elongated hollow ovary, producing ova from its epithelial lining, and thus agreeing very closely in structure with the testis.

In Glossiphonia, a fresh-water Rhynchobdellid, copulation in the ordinary sense of the word has never been observed, but one individual has been seen to deposit one or more spermatophores on any part of the body of another—often on the back. The

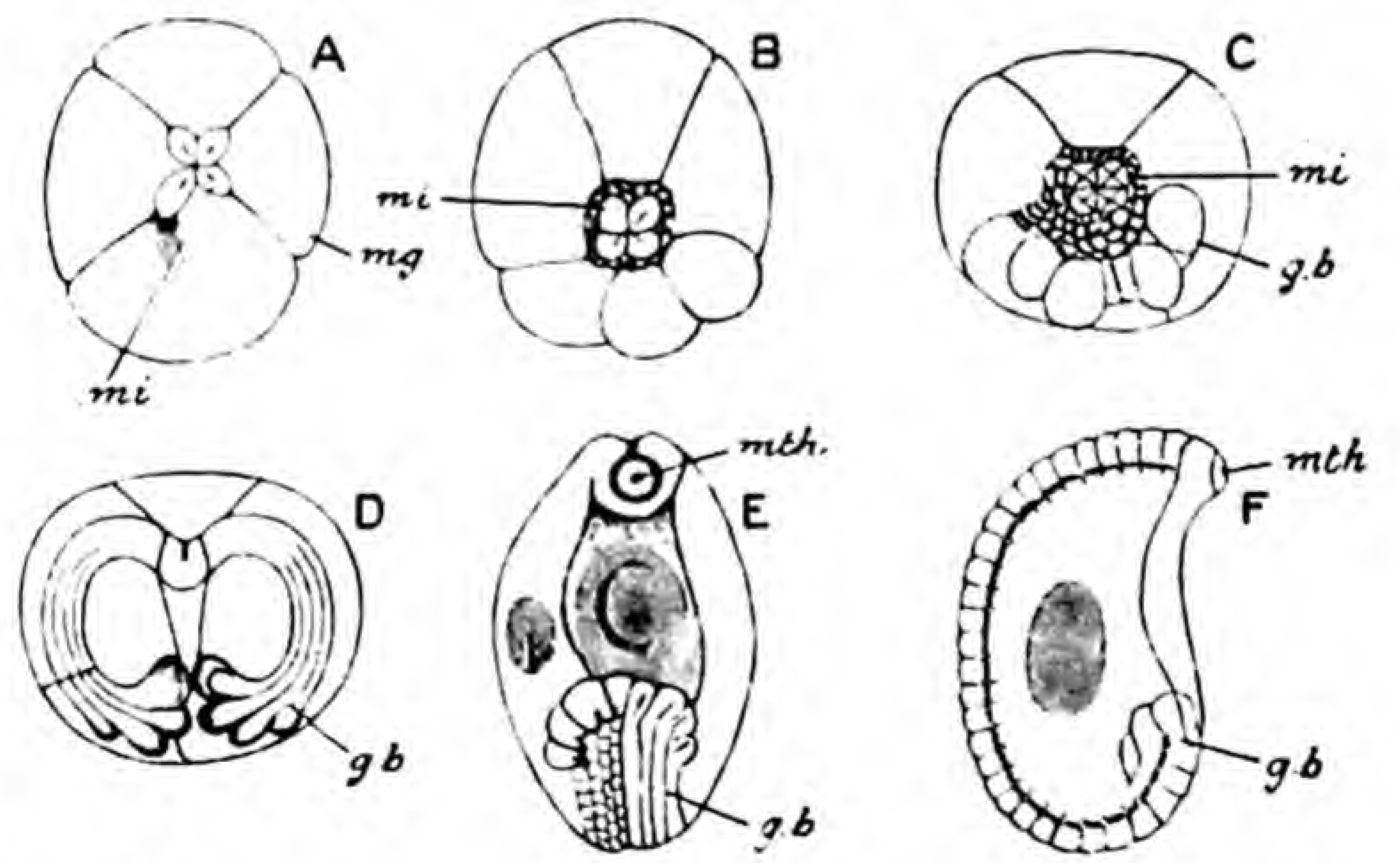


FIG. 331.—Six stages in the development of **Glossiphonia.** *g. b.* germinal bands; *mg.* macromeres; *mi.* micromeres; *mth.* mouth. (After Whitman.)

spermatophore, which is nearly 3½ mm. long, apparently exerts a solvent action on the skin, since, after a short interval, the spermatic substance streams through the skin into the cœlomic spaces, probably making its way at last to

the ovaries. This extraordinary process of *hypodermic impregnation* probably takes place in other genera, but has been most closely followed in Glossiphonia.

In Glossiphonia cleavage is unequal, the embryo consisting, in the eight-celled state (Fig. 331, *A*), of four large ventrally placed macromeres (*mg.*) and four dorsal micromeres (*mi.*). One of the macromeres, posterior in position, divides into two cells (*B*): the so-called *neuronephroblast* and *mesoblast*, the latter of which at once divides into two. As shown by their subsequent history, the neuronephroblast and the mesoblast correspond respectively to the first and second somatoblasts of Nereis. The former divides and subdivides to form two symmetrical groups of four cells each, situated at the posterior pole. The number of micromeres increases, at first apparently by division of the macromeres. The latter subsequently give off a number of small endoderm cells.

The embryo now consists of the three large macromeres with a number of endoderm cells, a cap of small micromeres forming an ectodermal layer which is extending over the surface, with, at the posterior pole, two symmetrical groups of neuronephroblast cells (four in each), and, somewhat deeper, the two mesoblast cells. From each of the ten cells last mentioned new cells are given off in front in such a way as to form ten rows of cells, five on each side, four being derived from neuronephroblasts and one from the mesoblast cell. These two sets of rows of cells constitute the so-called *germinal bands* (*g. b.*). From their subsequent fate it is clear that they correspond to the mesoderm bands of Nereis *plus* the neural plate. They grow forwards, the ectoderm extending with them, over the endoderm and macromeres. At first they diverge widely, but their anterior ends subsequently meet towards the anterior end of the embryo. Later the intermediate parts of the bands, originally widely separated from one another owing to their divergence during growth, approach one another and meet along the middle line of the ventral surface. The germinal bands give rise to the nerve-cord, the mesodermal segments, and the nephridia. The layer of micromeres not only gives rise to the whole ectoderm but also forms the head—the germinal bands not extending into that region. The embryonic enteric cavity (mesenteron) becomes formed by arrangement of the endoderm cells round the three macromeres, which break up to form nutrient material or yolk destined to become absorbed in nourishing the embryo. The pharynx is formed by an invagination of the ectoderm which joins the mesenteron. At this stage the embryo leaves the egg, and soon escapes from the cocoon to pass through its later stages attached to the ventral surface of the parent.

In the Gnathobdellida the young are hatched at an early stage of development, and their macromeres contain but little yolk: they are nourished up to the time of leaving the cocoon on the albumen with which the latter is filled. One member of this order, Herpobdella, is remarkable for undergoing a

metamorphosis: the anterior end of the embryo is ciliated, and it possesses a provisional pharynx and several pairs of provisional nephridia. Paired masses of cells, the *head-germs*, are developed in the head, and from these and the germinal bands the whole body of the adult is produced, the greater part of the larval body being cast off. This process resembles the development of the pilidium larva of certain Nemertines.

Habits, Distribution, etc.—The majority of the Hirudinea are inhabitants of fresh-water, and live, like the Medicinal Leech, by sucking the blood of higher animals—Vertebrates or Molluscs. It is doubtless in correlation with this intermittent parasitism—the chance of finding a vertebrate host being an infrequent one—that the crop has attained such vast dimensions, holding, in the case of the Medicinal Leech, as much blood as takes it a year to digest. The allied species *Hæmopis sanguisuga* has been found in the nasal passages of Man, producing serious results, and being, to all intents and purposes, an internal parasite. The same is the case with the Horse-leech, *Hæmopis vorax*, taken in, when young, by horses and cattle while drinking. It attaches itself to the pharynx and may even descend the trachea. Others are permanent ecto-parasites: for instance, *Branchellion* occurs on the outer surface of the Skate, Electric Ray, and other Fishes, entire families of this leech, including individuals of all sizes, being sometimes found crowded together on a small area of skin, which is distinctly marked by their powerful posterior suckers. Other fish-parasites are *Pontobdella*, on Rays, and *Piscicola*, on fresh-water Fish. Hæmopis is carnivorous, feeding on Snails and other Molluscs; so also are *Glossiphonia*, *Herpobdella*, and the gigantic *Macrobdella*. The last-named genus and some others are of subterranean habits, living in moist earth. The Land-leeches (*Hæmadipsa*) live in the forests of many parts of the world, and in spite of their small size, which does not exceed 30 mm. in length and 5 mm. in diameter, are much dreaded for the persistent attacks they make on men and cattle.

Many genera are very widely distributed: for instance, the Land-leeches (*Hæmadipsa*) occur in India, Ceylon, the East Indies, Japan, Australia, and South America, a distribution which seems to indicate that the group is one of great antiquity.

In adult structure, particularly in the absence of parapodia and setæ and the reduction of the cœlome, the Hirudinea differ markedly from the Chætopoda; but a study of their ealier developmental stages shows unmistakably their close connection with the latter group, more particularly with the Oligochæta; and the existence of an undoubted Leech (*Acanthobdella*) with setæ and with a well-developed cœlome traversed by mesenteries helps still further to bridge over the gap between the two classes.

CLASS III.—ARCHIANNELIDA.

More primitive in some respects than the other Annelida are the Archi-Annelida, comprising the families :—*Polygordiidæ, Protodrilidæ, Saccocirridæ, Dinophilidæ*, and *Nerillidæ*. *Polygordius* (Fig. 332, *A*) and *Protodrilus* (Fig. 333) are marine worms with a narrow, elongated, cylindrical body. The prostomium (Fig. 332, *Pr. st.*) is small, the peristomium (*Per. st.*) large. The

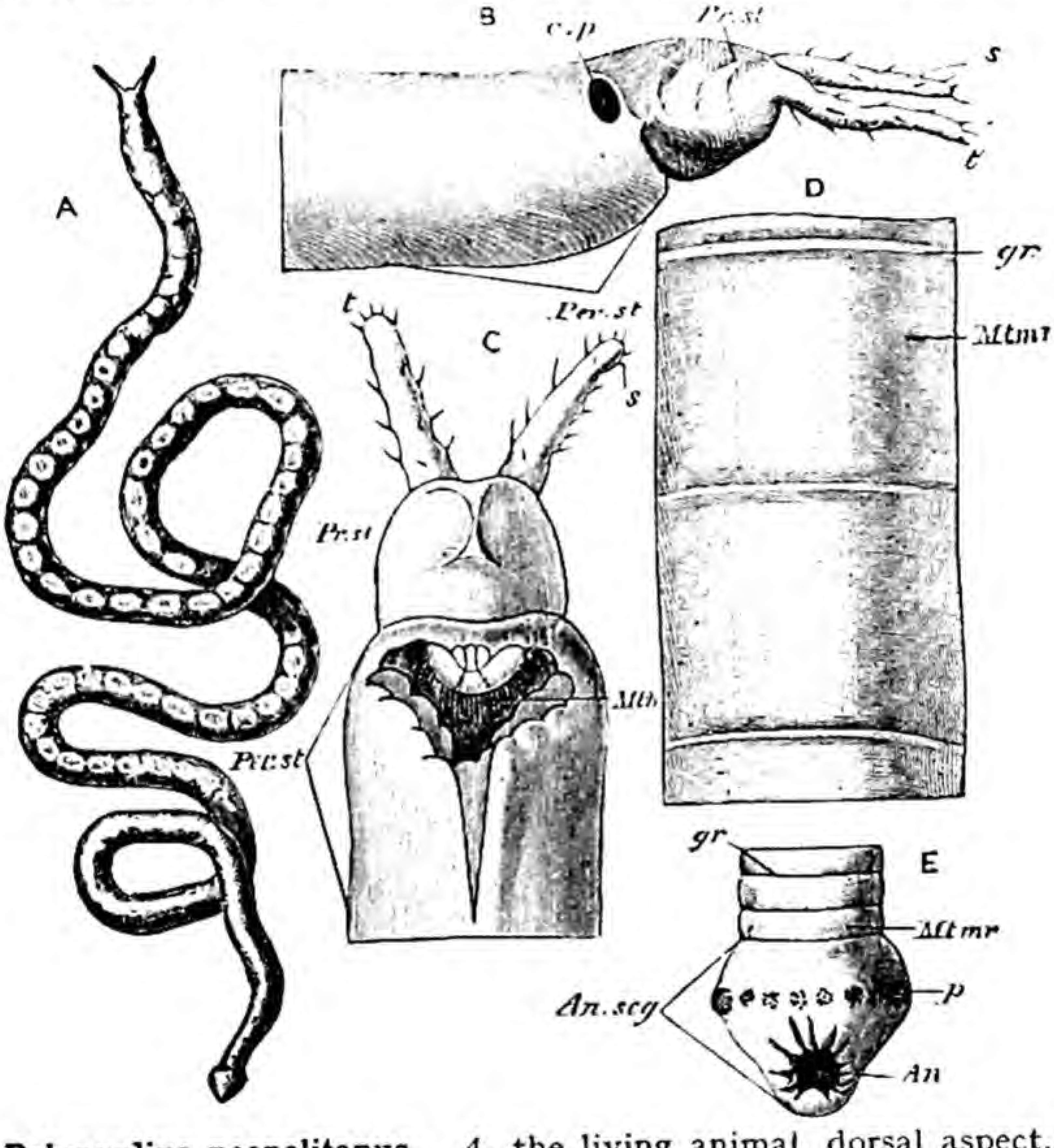


FIG. 332.—**Polygordius neapolitanus.** *A*, the living animal, dorsal aspect, about five times natural size; *B*, anterior end, lateral view; *C*, ventral view of the same; *D*, portion of the body showing the metameres; *E*, ventral view of the posterior extremity; *An.* anus; *An. seg.* anal segment; *c. p.* ciliated pit; *gr.* grooves between metameres; *Mth.* mouth; *Mtmr.* metameres; *p.* papillæ; *Per. st.* peristomium; *Pr. st.* prostomium; *s.* papillæ on tentacles (*t*). (From Parker's *Biology*, after Fraipont.)

segments (*Mtmr.*) are only faintly marked off externally for the most part, though the internal division of the cœlome by means of septa is complete. Parapodia and setæ are absent, but the prostomium bears a pair of tentacles (*t.*). Several pairs of simple nephridia are present. The position of the nervous system (Fig. 334) is more primitive than in the Annelida in general; it is continuous with the epidermis, and not separated from it by mesodermal elements as in most of the others. A pair of ciliated grooves (Fig. 332, B, *c. p.*) are probably to be looked upon as sense-organs.

There are a pair of prostomial tentacles, long in Protodrilus, short in Polygordius, and a pair of ciliated pits. The segmentation is only very indistinctly marked externally in Protodrilus by circlets of cilia; in Polygordius it is indistinct in front, but better marked behind. In *Polygordius lacteus* a series of tooth-like processes occurs round the anus, and in front a circlet of adhesive papillæ. In Protodrilus there is a ventral ciliated groove. There is a vascular system with dorsal and ventral longitudinal vessels. In each

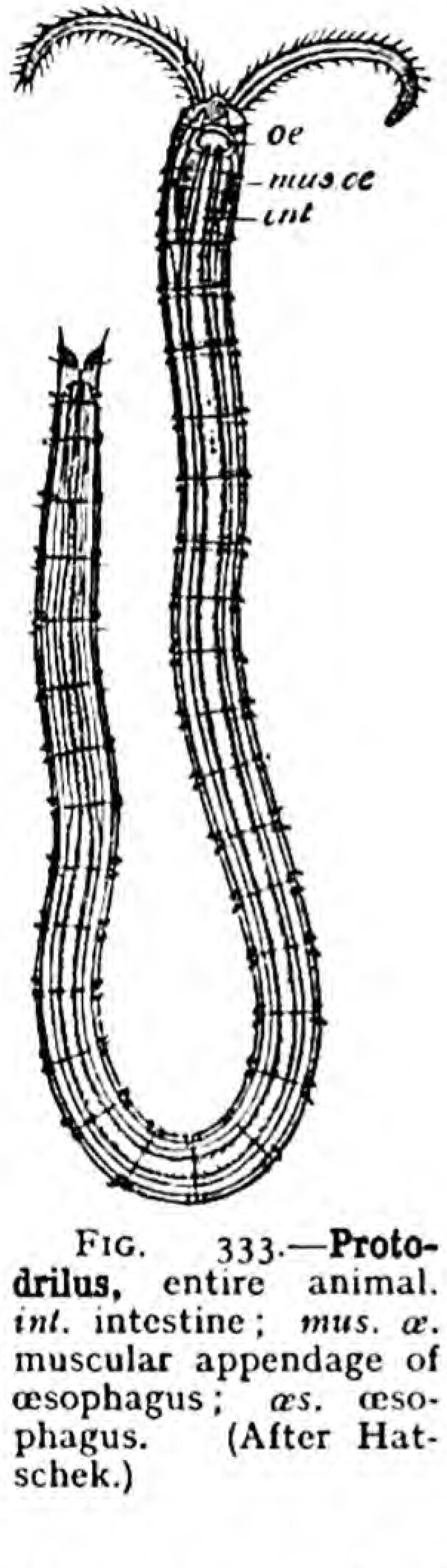


FIG. 333.—**Protodrilus**, entire animal. *int.* intestine; *mus. œ.* muscular appendage of œsophagus; *œs.* œsophagus. (After Hatschek.)

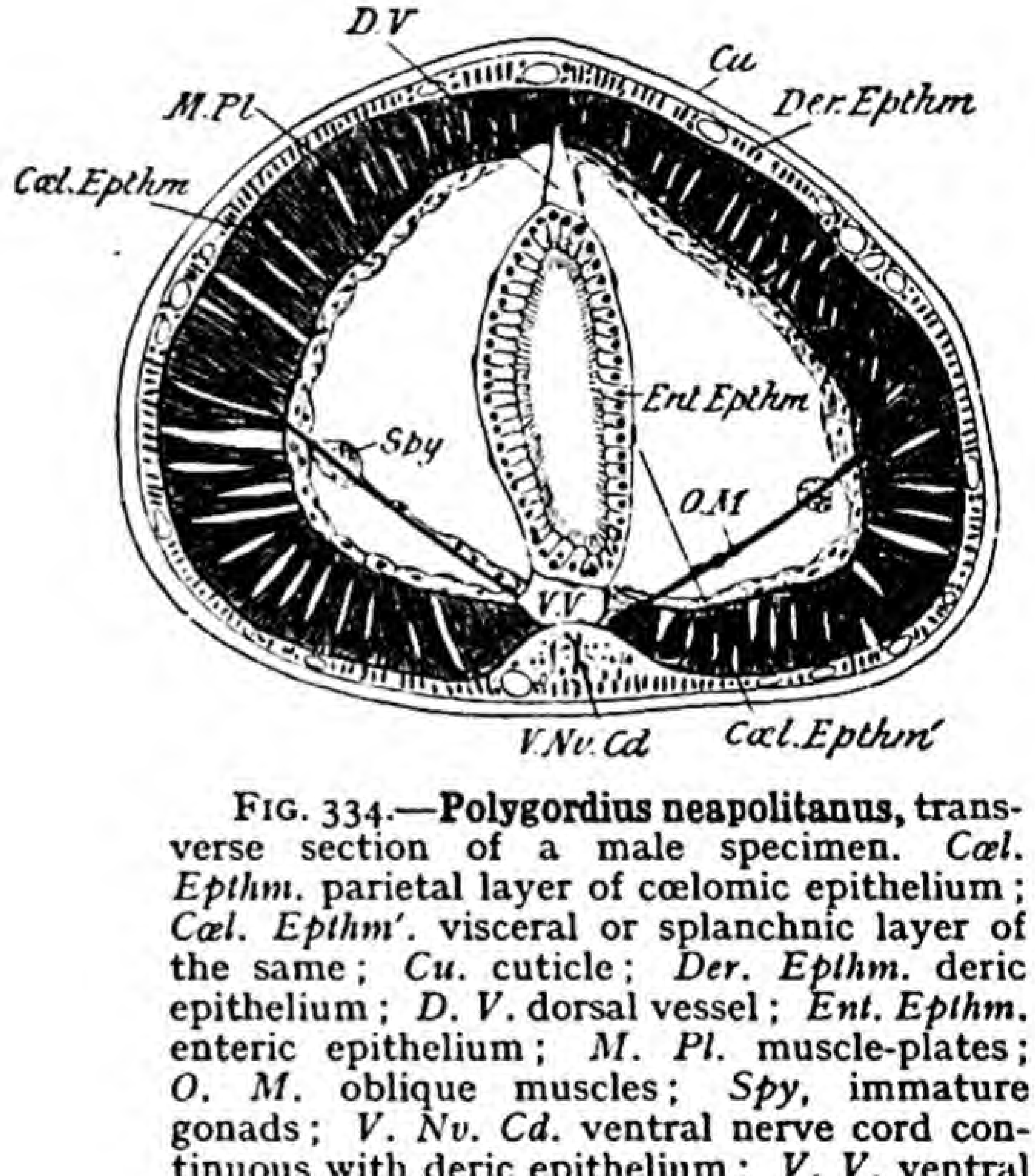


FIG. 334.—**Polygordius neapolitanus,** transverse section of a male specimen. *Cœl. Epthm.* parietal layer of cœlomic epithelium; *Cœl. Epthm'.* visceral or splanchnic layer of the same; *Cu.* cuticle; *Der. Epthm.* deric epithelium; *D. V.* dorsal vessel; *Ent. Epthm.* enteric epithelium; *M. Pl.* muscle-plates; *O. M.* oblique muscles; *Spy,* immature gonads; *V. Nv. Cd.* ventral nerve cord continuous with deric epithelium; *V. V.* ventral vessel. (From Parker's *Biology,* after Fraipont.)

segment is a pair of simple nephridia. In Protodrilus there are two ventral nerve-cords, connected together by transverse commissures: in Polygordius the cord (Fig. 334, *V. Nv. Cd.*) is single; in neither genus is there any trace of ganglia. The sexes are united in most individuals of Protodrilus, ovaries occurring in all the first seven segments and testes in some of those immediately following. In Polygordius the sexes are separate; the ovaries or testes (Fig. 334, *Spy*) are developed in the posterior segments. There are no special reproductive ducts.

The larva of Polygordius is a typical trochophore (Fig. 335), and its metamorphosis into the adult worm (Fig. 336) takes place as in the Polychæta in all essential respects.

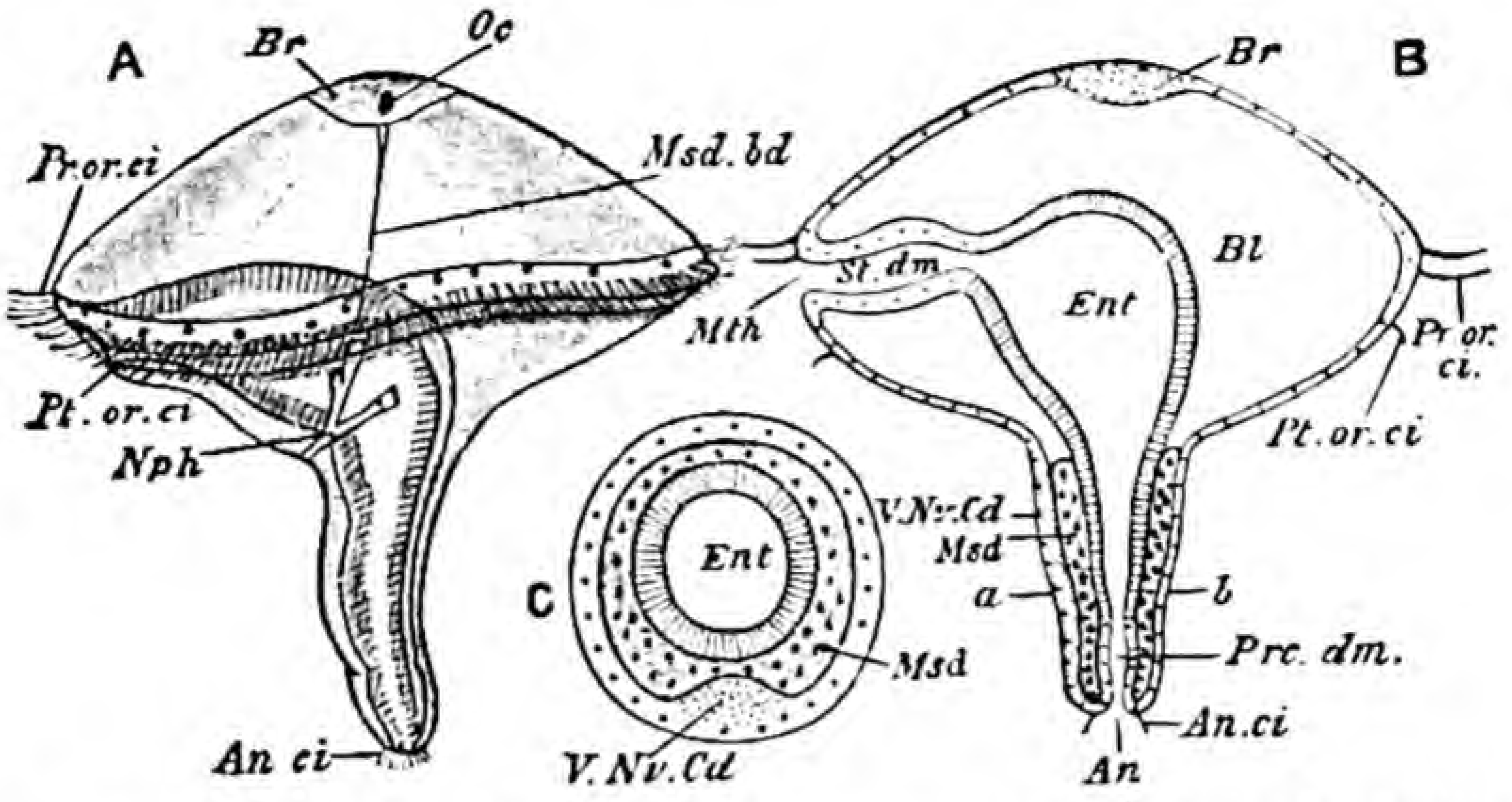


FIG. 335.—Trochophore of **Polygordius neapolitanus.** *A*, lateral view of entire larva; *B*, diagrammatic vertical section; *C*, transverse section through the plane *ab* in *B*; *An.* anus; *An. ci.* anal cilia; *Bl.* blastocœle; *Br.* apical plate; *Ent.* enteron; *Msd.* mesoderm; *Msd. bd.* mesodermal bands; *Nph.* excretory organ; *Oc.* eye-spot; *Pr. or. ci.* cilia of prototroch; *Prc. dm.* proctodæum; *Pt. or. ci.* post-oral cilia; *St. dm.* stomodæum; *V. Nv. Cd.* ventral nerve-cord. (From Parker's *Biology*, partly after Fraipont.)

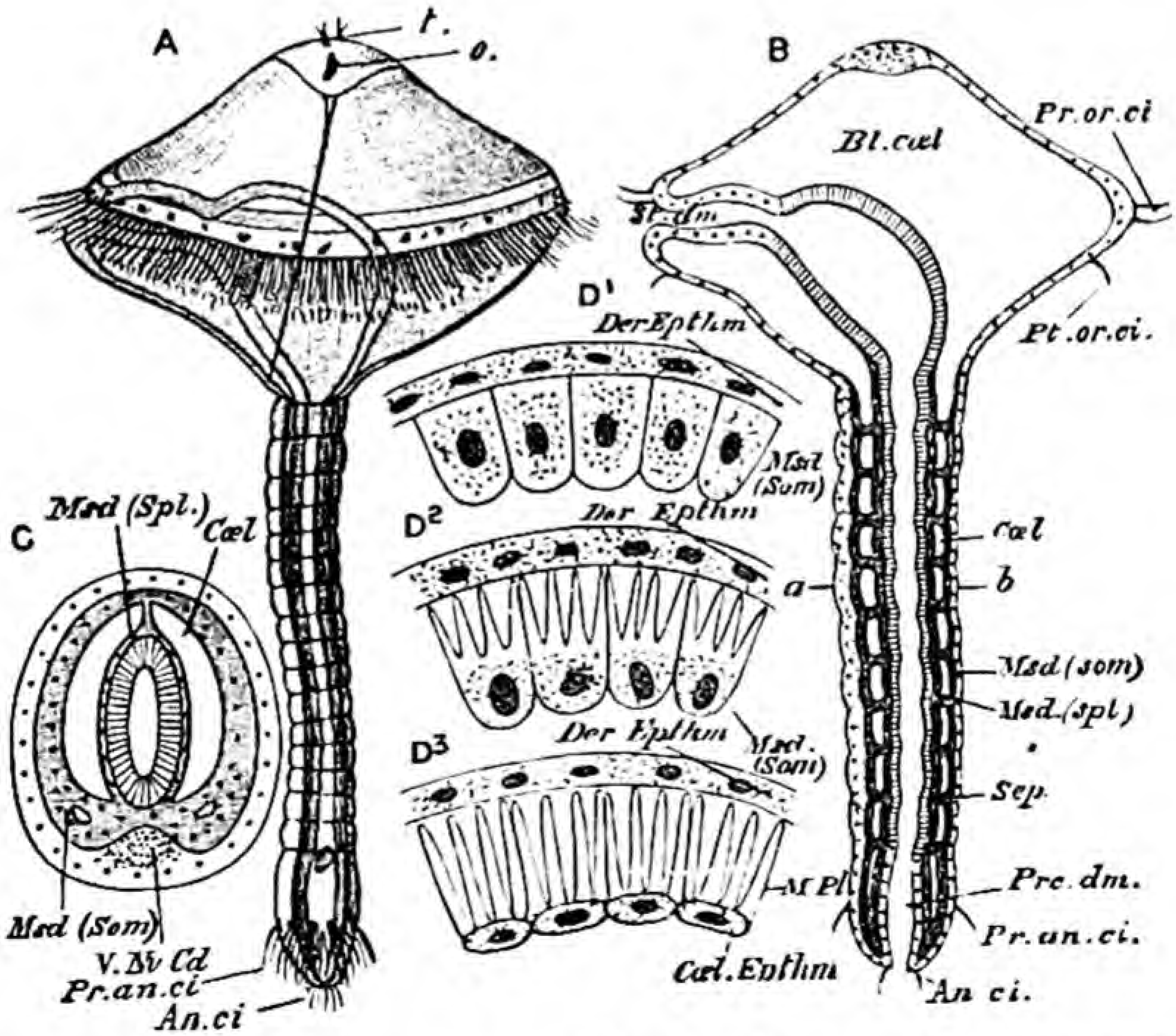


FIG. 336.—Later stage in the development of **Polygordius neapolitanus,** in which the posterior part of the trochophore has become elongated and segmented; *A*, entire larva; *B*, vertical section; *C*, transverse section along the plane *ab* in *B*; D^1—D^3, three stages in the development of the somatic mesoderm; *Cœl.* cœlome; *Cœl. Epthm.* cœlomic epithelium; *Der. Epthm.* deric epithelium; *M. pl.* muscle-plate; *Msd.* (*som.*), somatic mesoderm; *Msd.* (*spl*). splanchnic mesoderm; *o.* eye; *t.* tentacle. Other letters as in preceding figure. (From Parker's *Biology*, partly after Fraipont.)

Saccocirrus (Fig. 337) resembles Protodrilus. However, there are bundles of lateral chætæ on each segment. Two separate ventral nerve-cords lie immediately under the epidermis. The sexes are separate.

Nerilla (Fig. 338) is a minute marine worm with parapodia and chætæ and with hollow cirri. There are three prostomial tentacles and a pair of palps. The sexes are separate.

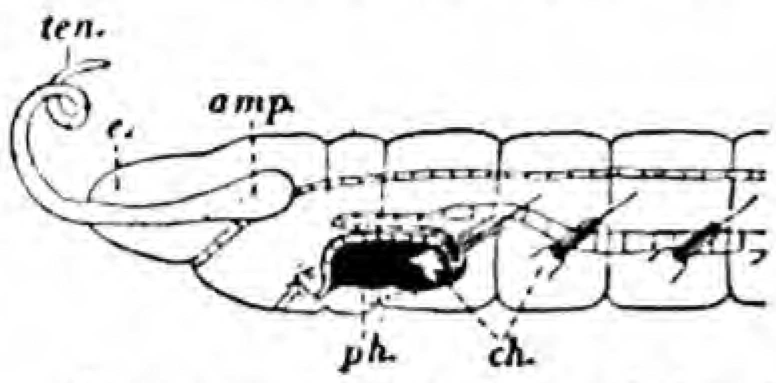


FIG. 337.—**Saccocirrus,** lateral view of anterior end. *amp.* ampulla of tentacle; *ch.* bundle of chætæ; *e.* eye; *ph.* pharynx; *ten.* tentacle. (From Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge), after Goodrich.)

Dinophilus (Fig. 339) too is a minute worm-like marine animal with a head or prostomium, a body composed of from five to eight segments separated from one another by constrictions, and a short

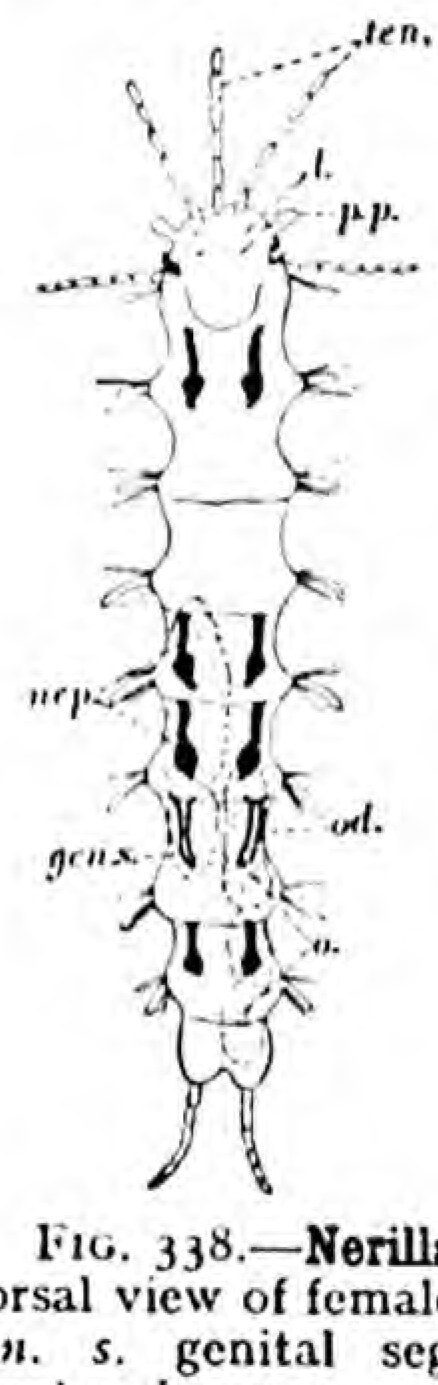


FIG. 338.—**Nerilla,** dorsal view of female. *gen. s.* genital segment; *l.* eyes; *nep.* nephridia; *o.* ovary; *od.* oviduct; *p. p.* palp; *ten.* tentacle. (From Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge), after Goodrich.)

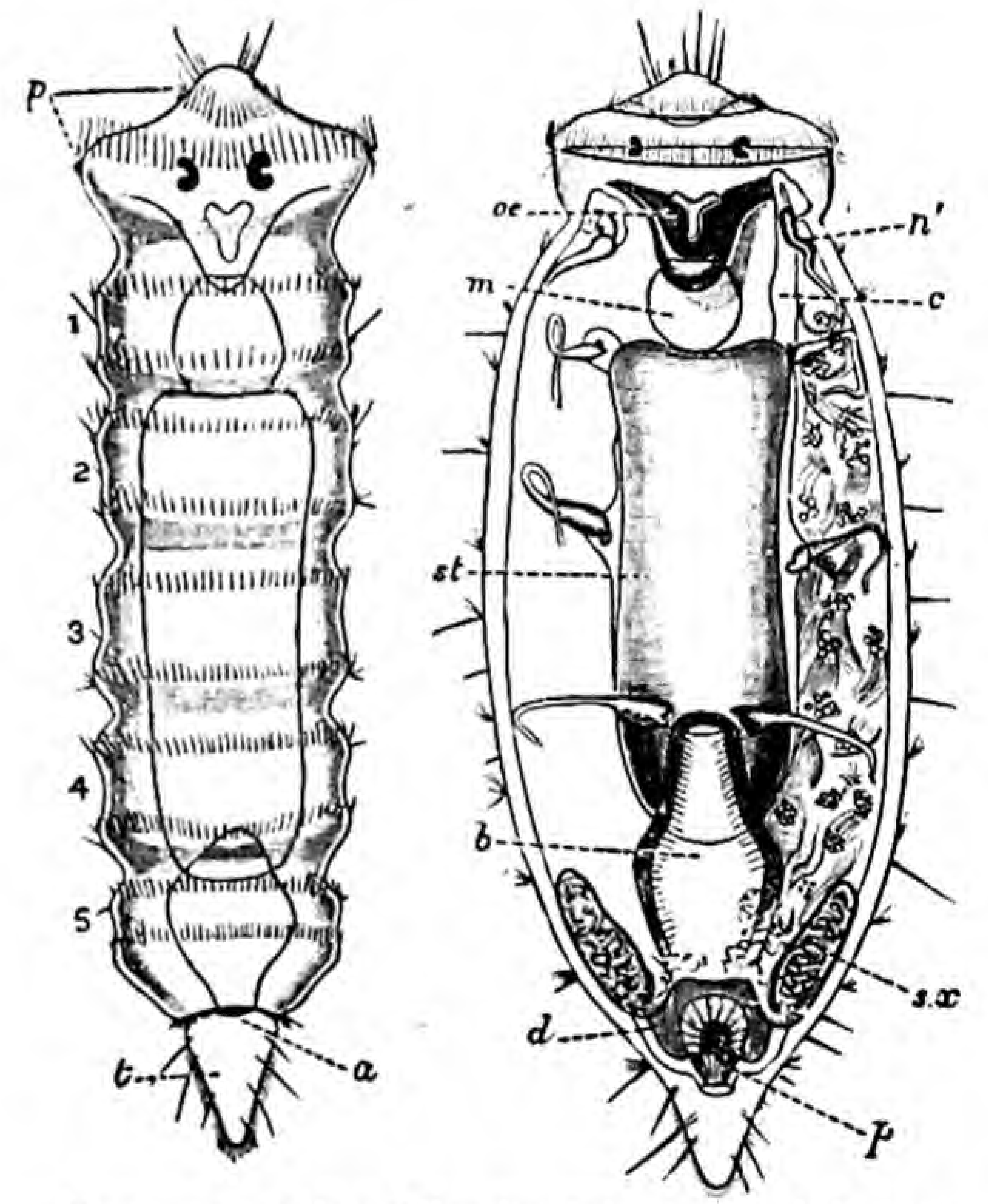


FIG. 339.—**Dinophilus tæniatus.** The left figure represents the dorsal surface of a young individual, × 76; the mouth and alimentary tract are seen by transparency. The right figure shows the anatomy of the male, × 38. *a.* anus; *b.* rectum; *c.* body-cavity; *d.* vas deferens; *m.* pharynx; *n'.* the first nephridium; *æ.* entrance to the œsophagus; *p.*, in left fig., prostomium; *p.*, in right fig., penis; *st.* stomach; *s. x.* vesiculæ seminalis. (From Sheldon, after Harmer.)

ventral tail. The prostomium bears two eye-spots and some sensory hairs: it is either covered uniformly with cilia, or bears two or three annular ciliated bands. The body is in some of the species uniformly ciliated; in others the cilia are disposed in rings corresponding to the segments, except on the ventral

surface, where the ciliation is always uniform. The mouth, which is situated on the ventral aspect of the prostomium, leads into an alimentary canal consisting of œsophagus, stomach, and intestine, all of which are ciliated; the anus (*a.*) is placed dorsally over the tail. A protrusible muscular proboscis lies, when retracted, in a recess opening close to the mouth. There is an imperfectly developed cœlome (hæmocœle?) which is crossed by strands of connective-tissue, and a ventral blood-vessel. A nervous system is present, and consists of a large dorsal ganglion in the prostomium, giving off two anterior and two posterior nerves or ventral cords (sometimes segmented into a series of ganglia connected in each segment by commissures), all situated in the epidermis.

The excretory system consists of a series of metamerically arranged pairs of tubes (*n.'*). The inner ends of these do not open into the body-cavity, but are provided with peculiarly modified flagellate cells known as *solenocytes*, so that these paired excretory tubes resemble closely the nephridia of some of the Polychæta. The sexes are separate. In the male there is a conical ventral penis; the last pair of nephridia act as vesiculæ seminales. In the ovary two sets of ova are developed, the larger destined to give rise to females and the smaller destined to form males. They pass into the body-cavity and reach the exterior by an aperture on the ventral surface in front of the anus.

APPENDIX TO THE ANNELIDA.

THE ECHIURIDA.

The Echiurida are a small group of marine worms, including the genera *Echiurus*, *Thalassema*, *Bonellia*, *Pseudobonellia*, *Hamingia*, *Saccosoma*, and *Epithetosoma*. They are unsegmented in the adult condition and have no parapodia, but, except in the case of Saccosoma, have a pair of ventral setæ in one or both sexes. The general shape is cylindrical or ovoid, with the mouth anterior and the anus posterior. Overhanging the mouth is a median appendage usually termed the *proboscis* (absent in Saccosoma). This is sometimes of great length, sometimes comparatively short, and is highly sensitive and mobile, but is not retractile. In some cases it contains a cavity communicating with the cœlome. There is a wide cœlome undivided by mesenteries, but crossed by numerous muscular strands which support the alimentary canal. The alimentary canal is a greatly coiled tube with a short thick-walled pharynx in front and an ovoid rectum behind. With the intestine communicates at both ends an elongated tube—the *siphon*, and a ciliated groove runs throughout its length. There is a closed blood-vascular system with a peri-intestinal sinus, a dorsal vessel, and a ventral vessel. The most important part of the nervous system (Fig. 342) takes the form of an unsegmented ventral nerve-cord giving off pairs of nerves. In front this bifurcates, and the two

cords resulting from the division running forwards past the mouth, extend throughout the length of the proboscis, at the anterior extremity of which they unite to form a great loop which shows no trace of ganglia. There are no sense-organs. Into the rectum open a pair of cæca—the *anal vesicles* which are probably the chief excretory organs. These have appended to them a number of ciliated funnels which open into them from the cœlome. Further forward there is a pair of nephridia, one of which may be aborted, or there may be two or three pairs. They function as gonoducts. The sexes are distinct and there may be extreme sexual dimorphism. The larva is a trochophore.

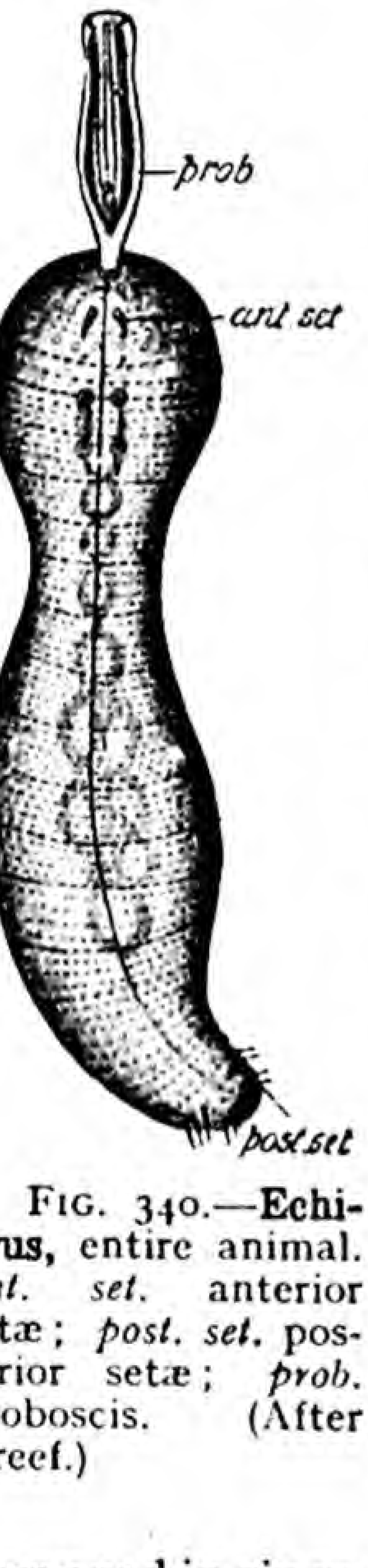


FIG. 340.—**Echiurus,** entire animal. *ant. set.* anterior setæ; *post. set.* posterior setæ; *prob.* proboscis. (After Greef.)

Echiurus (Fig. 340) is approximately cylindrical, with a moderately long proboscis which is excavated longitudinally on the ventral surface by a ciliated channel at the posterior end of which the mouth is situated. The surface is covered with small papillæ arranged in rings. On the ventral surface not far from the anterior end is a pair of short simple pointed setæ (*ant. set.*), each lodged in a setigerous sac and capable of being moved freely by means of appropriate muscles. Surrounding the posterior (*anal*) end of the body are a number of setæ (*post. set.*) arranged in one or two rings. The anal vesicles (Fig. 341, *an. ves.*) are narrow and elongated, and their funnels are sessile. There is a pair of nephridia (*neph.*) with nephrostomes and nephridiopores situated ventrally behind the setæ. The sexes are alike and the ovary or testis is a ventrally situated median mass of cells in the posterior half of the cœlome. The nephridia act as genital ducts.

Thalassema is allied to Echiurus, but has a shorter proboscis and no perianal setæ. There are from one to three pairs of nephridia.

Bonellia (Fig. 343) is ovoid in shape and green in colour, and is covered with large papillæ which are not arranged in rings. The proboscis is very long and very extensible, and bifurcated terminally. There are two ventral setæ, sometimes more. There is only one nephridium (Fig. 344, *neph.*) which is greatly enlarged and acts as a uterus. The anal vesicles (*an. ves.*) are ovoid, and the funnels terminate the branches of narrow branching tubes given off from the main vesicles. It is the female which has these characters: the male (Fig. 346) is minute, Turbellarian-like, ciliated, with in most species a pair of setæ, no proboscis, and a reduced alimentary canal without mouth or anus. In the young condition it enters the pharynx of the female and when sexually mature establishes itself permanently in the nephridium.

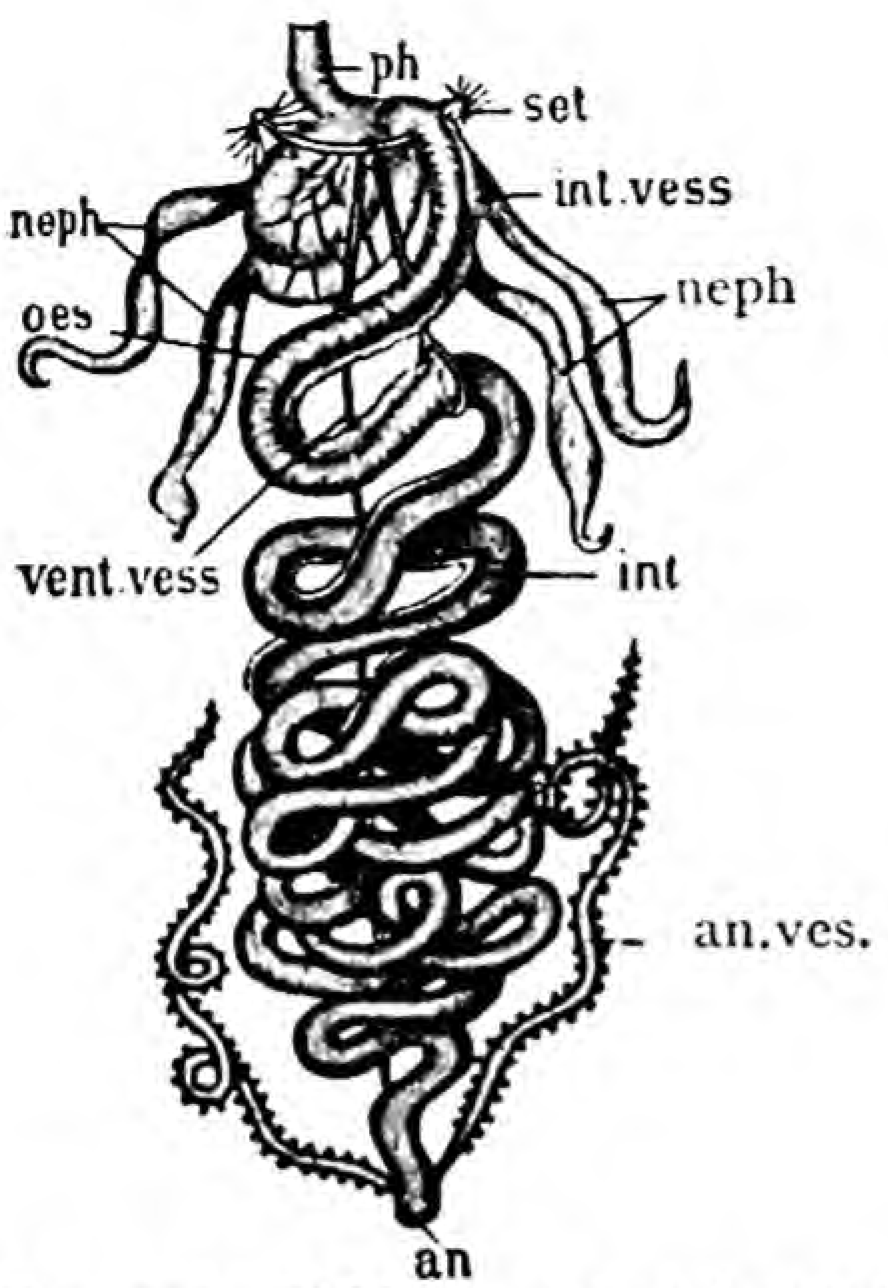


FIG. 341.—**Echiurus,** internal organization. *an.* anus; *an. ves.* anal vesicle; *neph.* nephridia; *int.* intestine; *int. vess.* intestinal vessel; *œs.* œsophagus; *ph.* pharynx; *set.* setigerous sacs; *vent. vess.* ventral vessel. (After Greef.)

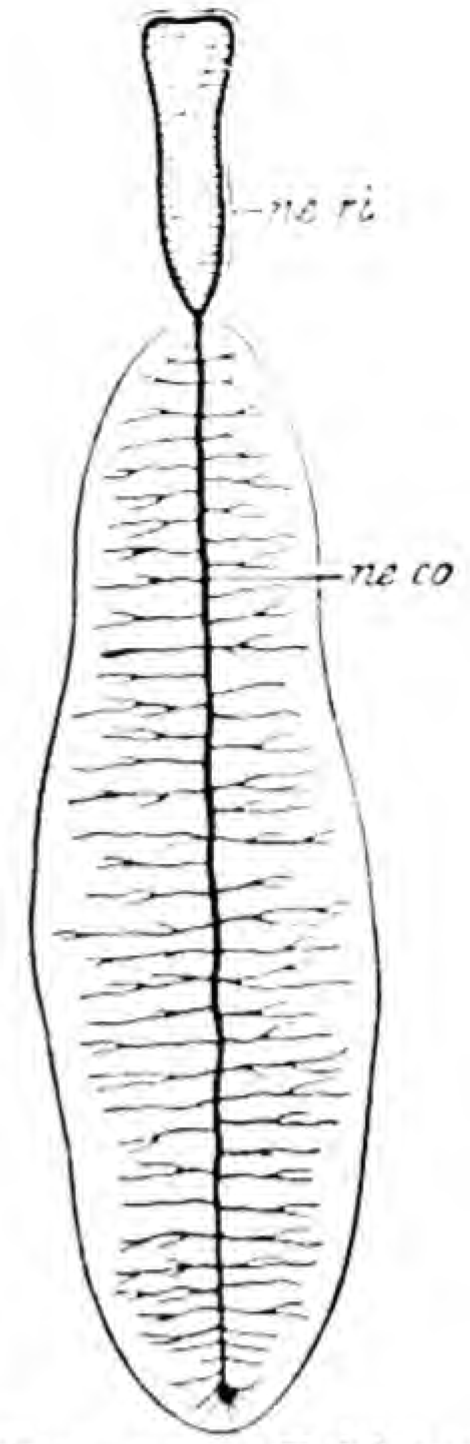


FIG. 342.—**Echiurus,** general outline of the animal, with the nervous system (diagrammatic). *ne. co.* nerve-cord; *ne. ri.* nerve-ring. (After Greef.)

FIG. 343.—**Bonellia viridis,** entire animal (female) with the proboscis moderately extended. (After Greef.)

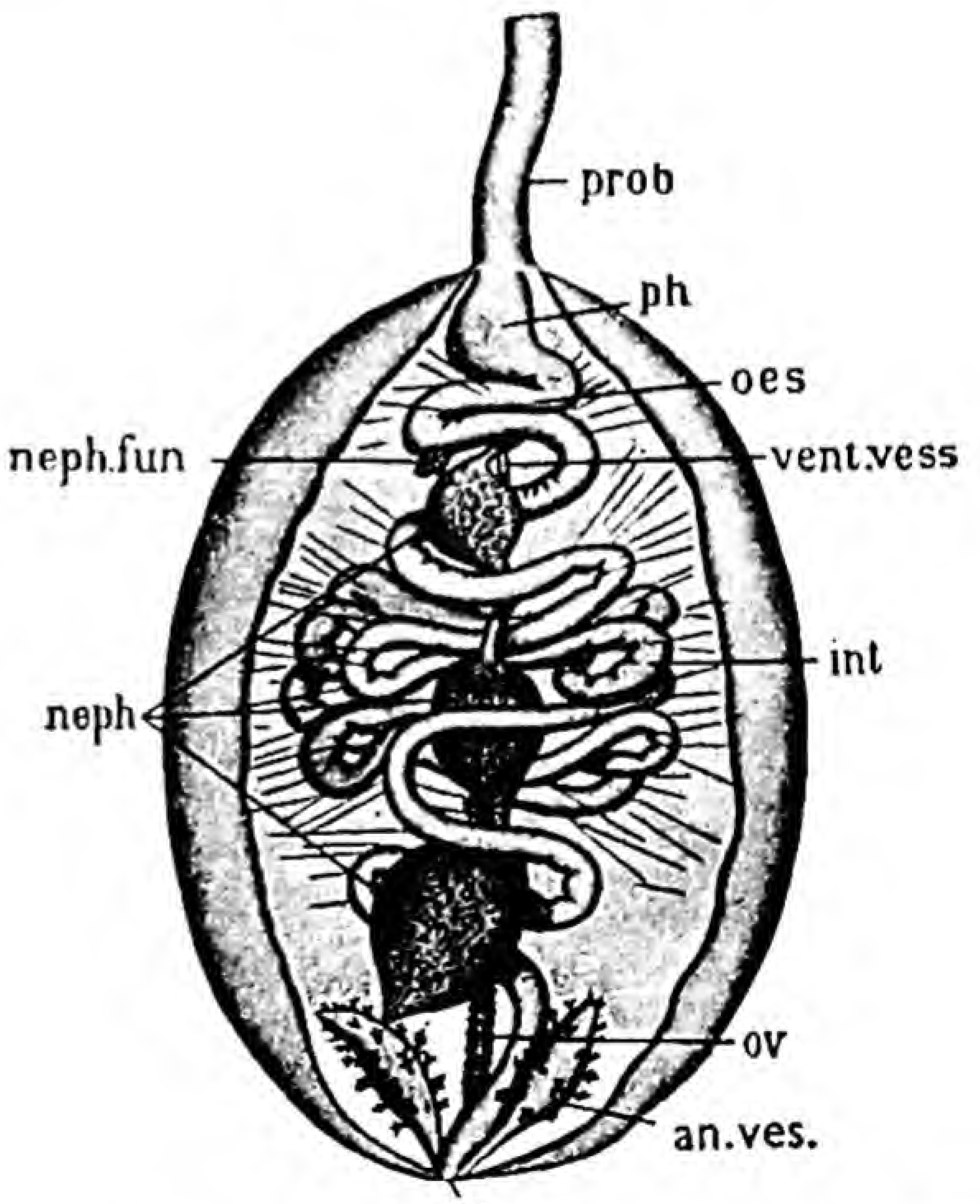


FIG. 344.—**Bonellia,** general view of the internal organs. *an.* anus; *an. ves.* anal vesicle; *neph.* nephridium; *int.* intestine; *neph. fun.* nephrostome; *œs.* œsophagus; *ov.* ovary; *ph.* pharynx; *prob.* proboscis; *vent. vess.* ventral vessel. (After Greef.)

Pseudobonellia is nearly related to Bonellia, but has two nephridia (uteri). The degenerate male, which has no setæ, lies in a median pit opening on the ventral surface between the two uteri.

Hamingia has a general resemblance as regards the female to Thalassema, but there are no setæ. There are two nephridia. The male, which has two setæ, is degenerate and parasitic in the female, as in Bonellia.

FIG. 345.—One of the ciliated funnels of the anal vesicles of Echiurus. (After Greef.)

Acanthohamingia has eight small setæ.

Epithetosoma has an extremely long filiform proboscis which, unlike that of the other genera, is hollow, containing a prolongation of the cœlome. There are no setæ. There is a single nephridium and no anal vesicles.

In *Saccosoma* both proboscis and setæ appear to be absent. The male is not known.

Development.—The larva of Echiurus (Fig. 347) has a well-developed pre-oral lobe with pre-oral and post-oral circlets of cilia, and in other respects closely resembles the trochophore embryo of a Chætopod. The posterior part of the body elongates, and the mesoderm-bands, developed as in the Chætopoda, become divided into as many as fifteen segments. A circlet of setæ is developed at the anal end, and subsequently

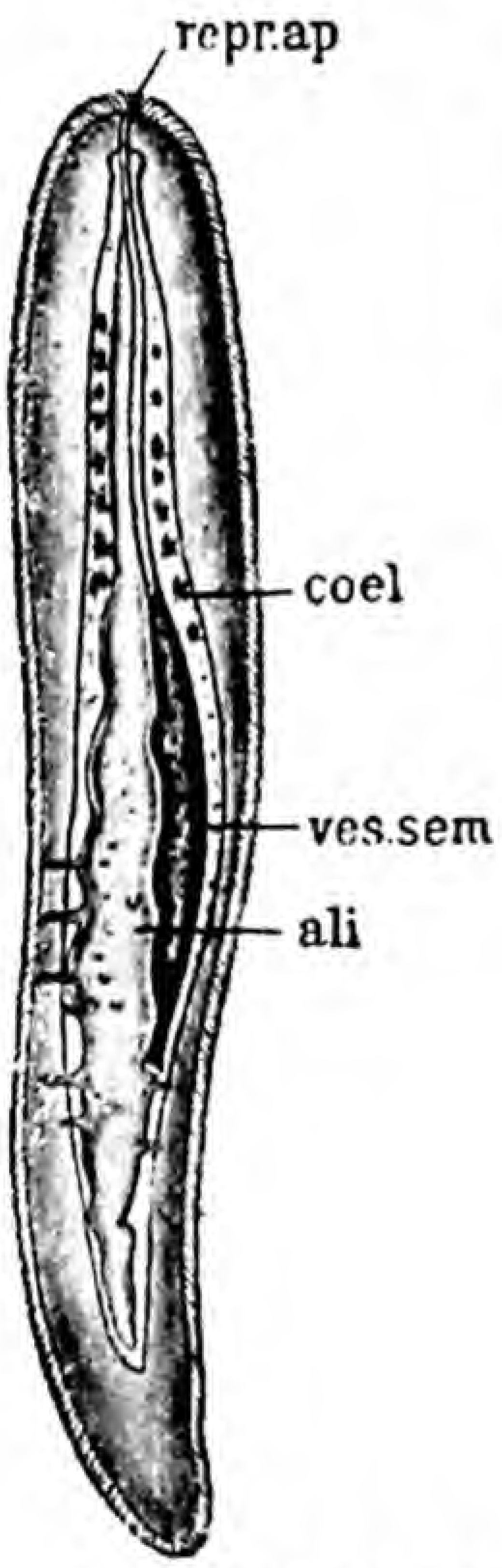


FIG. 346.—Male of **Bonellia.** *ali.* alimentary-canal; *cœl.* groups of cœlomic cells destined to give rise to sperms; *repr. ap.* reproductive aperture; *ves. sem.* vesicula seminalis. (After Greef.)

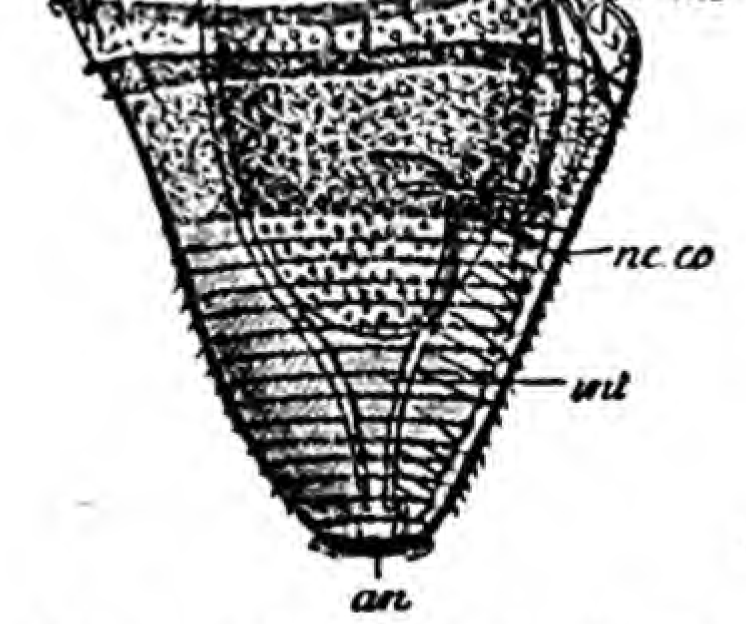


FIG. 347.—Trochophore of **Echiurus,** *an.* anus; *ap. pl.* apical plate; *int.* intestine; *mo.* mouth; *ne. co.* rudiment of nerve-cord; *œs.* œsophagus; *œs. conn.* œsophageal connective; *stom.* stomach. (After Hatschek.)

the two ventral setæ are formed in the same manner as in the Chætopoda. The pre-oral lobe becomes narrowed to form the cylindrical proboscis of the adult; and the rudimentary segmentation gradually disappears as development advances.

In Bonellia there is unequal spiral cleavage, as in most Annelida, resulting in the formation of four large macromeres and eight small micromeres: the latter multiply rapidly, and grow over the macromeres so as eventually to enclose the latter in a complete layer of ectoderm, save at one point, where there is a gap, the *blastopore*. Here the ectoderm bends inwards to give rise to a continuous mesoderm layer superficial to the macromeres. The blastopore soon closes up. The macromeres divide to form the cells of the endoderm, among which a lumen only appears comparatively late; mouth and œsophagus are developed as an outgrowth, at first solid, from the endoderm. The anus becomes formed still later by invagination at the hinder end of the body; and a pair of epidermal vesicles which appear at its sides, developed as outgrowths from the terminal part of the intestine, form the rudiments of the anal vesicles. A rudimentary pre-oral lobe becomes established. The mesoderm remains unsegmented, but splits into somatic and splanchnic layers going to form the muscular system, blood-vessels, and other mesodermal organs. Before the alimentary canal is formed, the larva, which had previously been spherical with two bands of cilia and a pair of eye-spots, becomes elongated and dorso-ventrally compressed, and covered uniformly with cilia, so as to present the general appearance of a Planarian. A high percentage of these larvæ are sexually indifferent, *i.e.*, they can either develop into female or into male adults. They may become converted into the adult female by a metamorphosis, including the elongation of the pre-oral lobe to form the proboscis and the development of the pair of setæ of the adult. If, however, the larvæ come into contact with the proboscis of an adult female, they adhere to it and consequently develop into males. The male never goes through the metamorphosis but becomes sexually mature in the larval stage. The stimulus for male-development is a chemical one, derived from the proboscis of the adult female. It appears to inhibit growth and female metamorphosis and to cause the development of male reproductive organs. The minute males enter the œsophagus of the females and, when sexually mature, pass into the cavity of the uterus.

THE SIPUNCULIDA.

The *Sipunculida* are marine worm-like animals devoid of any trace of segmentation in the adult condition, without parapodia, and without setæ; with an invaginable anterior body-region or introvert, at the extremity of which is the mouth surrounded by tentacles. The anus is anterior and dorsal. There

is an extensive cœlome filled with a corpusculated fluid, and not divided by septa. The ventral nerve-cord is not made up of a series of ganglia. There is, as a general rule, only a single pair of nephridia. The sexes are separate; the ovaries and testes simple masses of cells; the nephridia act as reproductive ducts. The larva is a modified trochophore.

1. Example of the Class—*Sipunculus nudus.*

General External Features.—*Sipunculus* occurs on sand at moderate depths off the coast in most countries outside of the tropics. It is an elongated worm of a cylindrical shape, somewhat narrower towards one—the anterior—end. There is no trace of division into segments. The anterior portion of the body,

Fig. 348.—Anterior extremity of **Sipunculus nudus.** *ant. pap.* anterior papillary region; *post. pap.* posterior papillary region; *tent.* tentacular fold. (After Ward.)

Fig. 349.—Tentacular fold of **Sipunculus nudus.** *cer. org.* cerebral organ. (After Ward.)

to the extent of about a sixth of the total length, is capable of being involuted within the part behind. The surface of this anterior part, which is termed the *introvert* (Fig. 348), differs in appearance from that of the rest of the body in being covered more or less closely with chitinous papillæ. The papillæ of the posterior portion of the introvert are shaped like the bowl of a spoon, with the concavity turned towards the body-wall and the tip directed backwards; they are so closely arranged as to overlap one another like the shingles of the roof of a house: further back they become longer and narrower, mammilliform, and more scattered. When the introvert is fully evaginated, there appears at its extremity a horse-shoe-shaped fold of the integument, the *tentacular fold* (*tent.*), which is lobed and plaited (Fig. 349) so as to assume somewhat the appearance of a circlet of tentacles. For a little space immediately behind

the tentacular fold the surface of the introvert is free from papillæ. The posterior portion of the body is devoid of papillæ, but is marked out by a series of narrow impressed lines into a number of elongated four-sided areas.

Body-wall.—The surface is covered by a chitinoid *cuticle* having an iridescent lustre similar to that presented by the cuticle of Nereis and Lumbricus, and due to the same cause—viz., the presence of two systems of intercrossing lines. The papillæ on the introvert are local thickenings of this cuticular layer. Beneath the cuticle is an *epidermis* consisting of a single layer of cells, usually sac-like, but capable of being altered as a result of contraction or compression

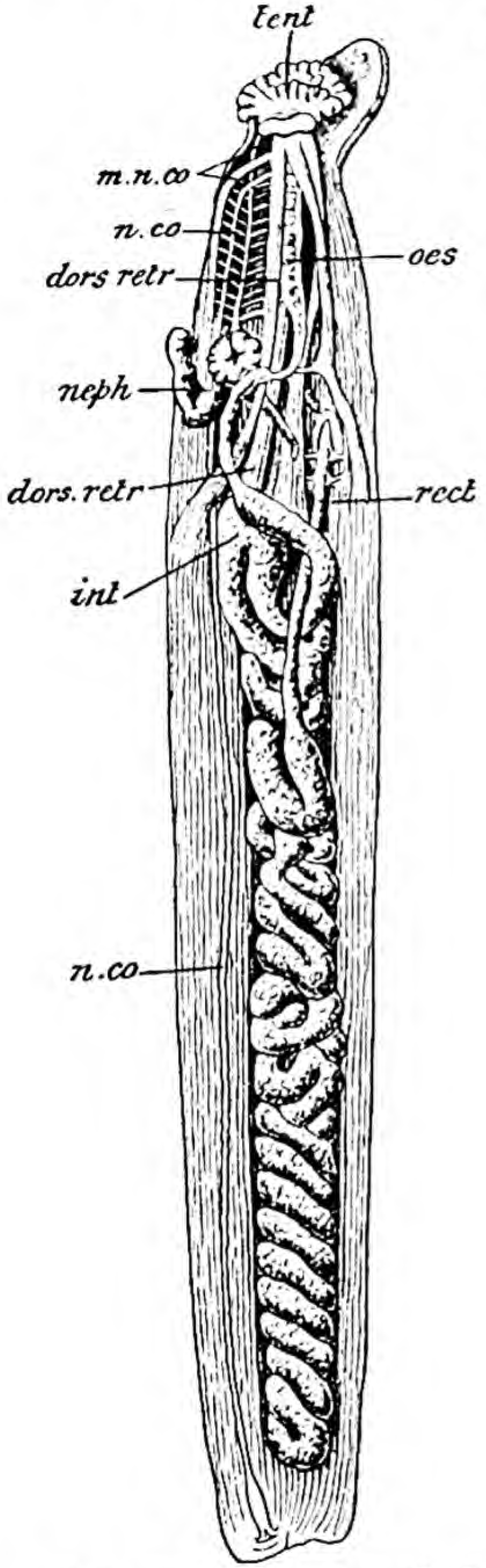


FIG. 350.—Dissection of the internal organs of **Sipunculus nudus.** *dors. retr.* dorsal retractor muscles of the introvert; *int.* intestine; *m. n. co.* muscles accompanying the nerve-cord; *n. co.* nerve-cord; *neph.* nephridium; *œs.* œsophagus; *rect.* rectum; *tent.* tentacular fold. (After Vogt and Jung.)

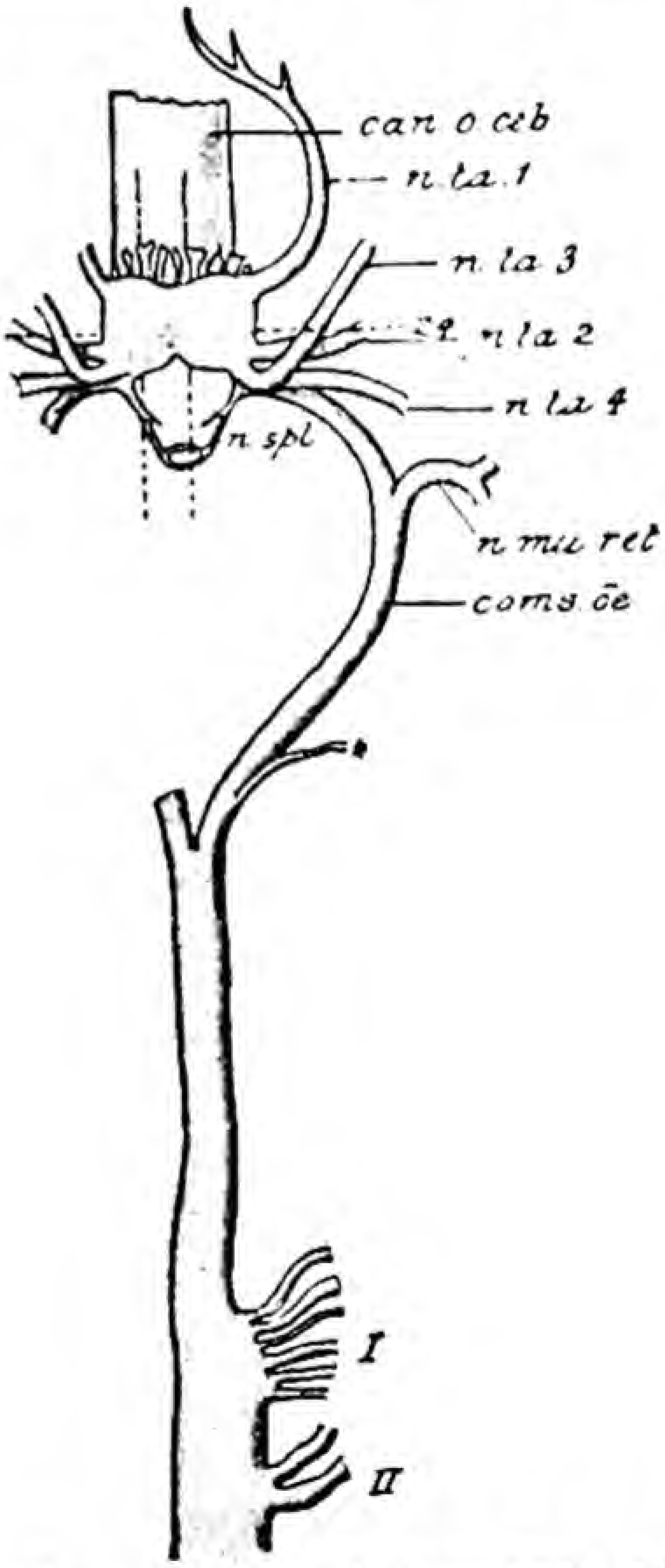


FIG. 351.—Anterior part of the nervous system of **Sipunculus nudus.** *can. o. ceb.* cerebral organ; *coms. œ.* œsophageal connective; *n. mu. ret.* nerves to retractor muscles; *n. spl.* splanchnic nerves; *n. ta, 1–4,* nerves to tentacular fold; *I, II,* nerves from ventral cord; *24,* main mass of brain. (After Ward.)

into a spindle-like shape. Below the epidermis is a layer of connective-tissue, the *dermis*, in which, as well as to some extent in the epidermis itself, are a number of *dermal bodies*. Of these there are three kinds—*bicellular glands*, contained in papillæ; *multicellular glands*, scattered through the integument and not contained in papillæ; and *sense-papillæ*, small, rounded thickenings of the epidermis in the anterior region of the introvert, with their summits covered with cilia. There are also numerous pigment-cells. A number of canals branch through the dermis, beneath which are three layers of muscle—(1) an outer *circular* layer, continuous in the introvert, but divided into annular bands in the rest of the body; (2) an *oblique* layer, well developed only between the origins of the two retractor muscles of the introvert; (3) a *longitudinal* layer, which is separated by spaces into a series of parallel bands. Between the bundles of the longitudinal layer of muscles runs a system of canals which communicate with the body-cavity by transverse branches.

There is a spacious **cœlome**, but it is traversed in all directions by filaments and strands of connective-tissue, with which are mixed very fine muscular fibres; these mostly run from the wall of the body to the alimentary canal. Floating in the cœlomic fluid are (1) colourless amœboid corpuscles; (2) rounded biconcave corpuscles, faintly coloured by a substance, *hæmerythrin*, which has, however, no demonstrable respiratory function; (3) reproductive elements; (4) peculiar unicellular ciliated bodies, the *urns*, which are developed by proliferation from cells on the wall of the dorsal blood-vessel. These are comparable in structure and function with the ciliated funnels of the Hirudinea.

The **blood-vascular system** is very feebly developed. It consists of *dorsal* and *ventral* contractile vessels, the former known as the "heart," communicating in front with a *circular sinus* at the base of the tentacular fold.

The **alimentary canal** (Fig. 350) is a cylindrical tube of uniform character throughout. It is twice the length of the body, running back from the mouth towards the posterior end, and then bending sharply round to run forwards to the anus, the two limbs being twisted spirally round one another. Running along the inner surface of the entire length of the alimentary canal, with the exception of the terminal part or rectum, is a narrow groove. Connected with the rectum is a narrow *cæcum* of variable length, which opens into the beginning of the rectum. Two tuft-like groups of *rectal glands* occur close to the anal opening.

The **nervous system** (Fig. 351) differs considerably from that of the Annelida. There is a relatively small bilobed *cerebral ganglion* situated on the dorsal aspect just behind the tentacular circlet, to which it gives off on each side several pairs of nerves. Arising from it anteriorly and dorsally are a number of digitate processes lying in the cœlome. The *œsophageal connectives* (*coms. œ*) which it gives off behind are greatly elongated; from each arise *muscular* nerves (*n. mu. ret*), and also a *visceral* nerve (*n. spl*) passing to the alimentary canal.

The two commissures unite behind to form a *ventral cord*, which extends throughout the rest of the length of the body. The ventral cord presents no appearance of ganglia: it sends off laterally a large number of pairs of nerves (*I.*, *II.*); on section it appears distinctly double. Two delicate muscular bands (Fig. 350, *m. n. co.*), which take origin anteriorly from the body-wall, become attached to the nerve-cord, and follow it throughout its length, giving off small branch-bands to accompany the lateral nerves. A canal with ciliated, folded and pigmented walls, which opens in the middle line of the dorsal surface just behind the tentacular fold (Fig. 349, *cer. org.*), extends backwards to the anterior ventral surface of the cerebral ganglion, where it ends blindly. It is possible that this, the *cerebral organ*, may be a sensory organ of some kind. *Eyes* are wanting. The digitate processes of the cerebral ganglion, which bear a number of ciliated cups along their edges, may be sensory in character.

Sipunculus has only a single pair of **nephridia**. These (Fig. 350, *neph.*) are situated tolerably far forwards, the external openings being about 2 cm. in front of the anus. They are long, nearly straight tubes, of a brown or yellowish colour, and very mobile in the living condition. Near the external opening, which is situated at the anterior end, is the internal opening into the cœlome. The sexes are separate. There are no definite **gonads** except at a certain season of the year, when cellular elevations developed in the connective tissue covering the ventral retractor muscles of the introvert represent *ovaries* or *testes* as the case may be. These give origin to cells which become detached and develop into the fully-formed sexual elements while floating about in the cœlomic fluid. The nephridia act as *gonoducts*.

2. Distinctive Characters.

The Sipunculida are worms with the body devoid of any appearance of segmentation in the adult condition. There is a large cœlome, which is not divided into chambers by mesenteries or septa. A blood-vascular system is sometimes present, sometimes absent. The ventral nerve-cord is not composed of a chain of ganglia. There is usually only one pair of nephridia. The sexes are separate, the gonads simple, and the nephridia act as gonoducts.

The larva is in most cases a trochophore. The early stages of the development closely resemble those of the embryo of one of the Polychæta, and a stage corresponding to the trochophore of that class is developed, but with the mouth situated further forward in front of the ring of cilia and with the anus in front of the posterior extremity on the dorsal side. At no stage in the development has any trace been observed of the temporary segmentation which forms so marked a feature in the development of Echiurus. But in at least one member of the group (Phascolosoma gouldi) the mesoderm undergoes temporary segmentation, and the cœlome is formed by the coalescence of cavities which appear in these segments.

3. Distribution, Affinities, Etc.

The Sipunculida are all marine. They are only capable of very slow creeping locomotion, and live for the most part either in natural rock-fissures, or in interstices between masses of fixed animals such as Mussels or Ascidians, or in discarded shells of Mollusca or tubes of Polychæta, or in burrows which they excavate for themselves either in sand or mud, coral or rock. Their distribution is general; and they occur at considerable depths as well as in shallow water.

The resemblances between the Sipunculida and the Echiurida have been and are regarded by many authors as sufficiently important to justify the inclusion of both in one class to which the name Gephyrea was given. But apart from the embryological history, the introvert of the Sipunculida with its crown of tentacles, the forward dorsal position of the anus, and the absence of true setæ are all points in which the members of that class diverge far from the Echiurida.

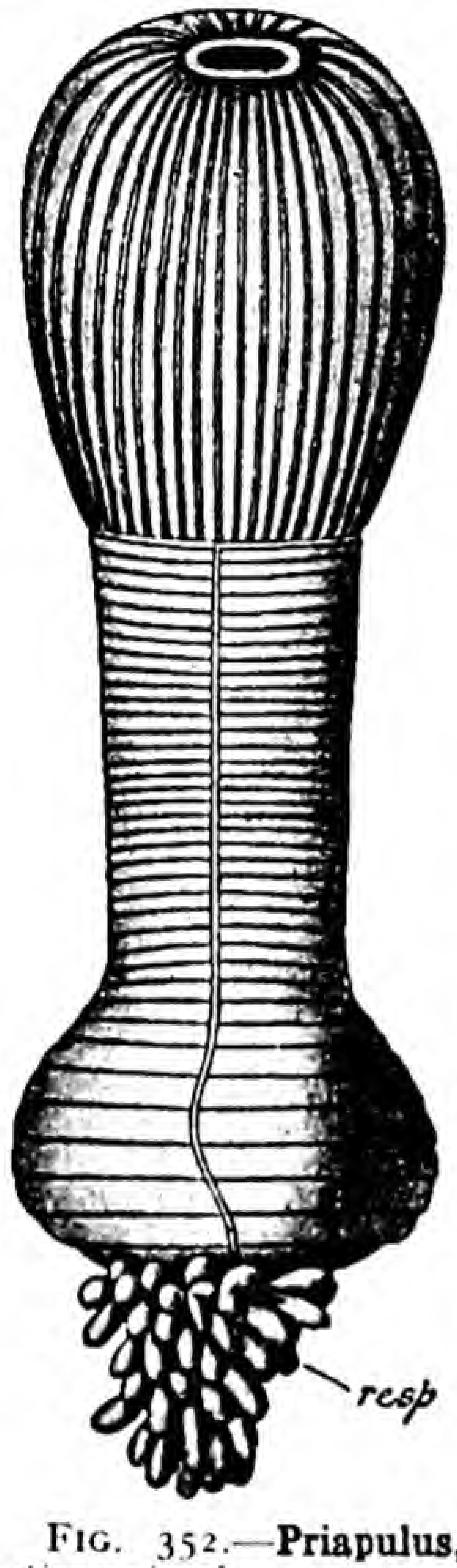


Fig. 352.—**Priapulus,** entire animal. *resp.* posterior papillæ. (After Ehlers.)

The *Priapulida*, often classed in connection with the Sipunculida, may be mentioned here. *Priapulus* (Fig. 352), species of which have been found widely distributed at moderate depths in extra-tropical seas, is a cylindrical worm, unsegmented but with numerous superficial annulations in the posterior half. At the anterior end is the mouth and at the posterior the anus. There is a short introvert, but no oral tentacles or tentacular fold. At the posterior end is a hollow single or double process beset with hollow papillæ (*resp.*): the lumen of this is in communication with the cœlome, and the whole apparatus is doubtless a respiratory organ or *branchia*. The alimentary canal, which is not coiled, consists of a muscular pharynx, a thin-walled intestine, and a rounded rectum. There is no blood-vascular system. The nervous system is in close connection with the epidermis: it consists of a simple ventral nerve-cord and a circum-œsophageal ring without brain-enlargement. The sexes are distinct. The ovaries or testes are a pair of masses of follicles each having its main duct which opens on the exterior close to the anus. The genital ducts with their branches seem to act as excretory organs. The development of Priapulus is unknown.

SECTION VIII

PHYLUM ARTHROPODA

In this large and important group of animals we meet with a characteristic feature of the Chætopoda, viz. metameric segmentation, and also with more or less perfect bilateral symmetry; the mouth and anus are at opposite ends of the elongated body, and the central nervous system consists of a dorsal brain and a double ventral chain of ganglia. There is, however, an important advance on the segmented Worms in the circumstance that each typical segment bears a pair of appendages, distinguished from the simple foot-stumps or parapodia of the Polychæta in being divisible into distinct limb-segments or *podomeres*, separated from one another by movable joints and acted upon by special muscles. Arthropods are also characterized by the universal absence of cilia, by their muscles being always of the striped kind, and by the body-cavity largely corresponding not to a true cœlome, but to a *hæmocœle*, in free communication with the circulatory system and developed from the latter.

The following are the most important subdivisions of the phylum :—

Class 1. CRUSTACEA, including Crayfishes, Crabs, Shrimps, Wood-lice, Barnacles, Water-fleas, etc.

Class 2. MYRIAPODA, including the Centipedes and Millipedes.

Class 3. INSECTA, including the six-legged Insects, such as Cockroaches, Locusts, Flies, Beetles, Butterflies, and Bees.

Class 4. ARACHNIDA, including Spiders, Scorpions, Mites, etc.

The ONYCHOPHORA will be dealt with in an appendix to this phylum.

CLASS I.—CRUSTACEA.

1. EXAMPLES OF THE CLASS.

a. Apus or Lepidurus.

Apus and Lepidurus are two closely allied Crustaceans found in the fresh-waters of most parts of the world, but curiously local in distribution and by no means common. They are so much alike that, save in minor details, the same description will apply to any species of either genus.

External Characters.—The animal (Fig. 353) is from 20 to 30 mm. in length, and has the anterior two-thirds of the dorsal surface covered by a thin chitinous

shell or *carapace*, beyond the posterior edge of which the hinder part of the body (*abd.*) projects as a nearly cylindrical structure distinctly divided into segments. The last or *anal segment* bears a pair of long processes, the *caudal styles* (*a. f.*), between which, in Lepidurus, is a flat scale-like *post-anal plate* (Fig. 354). On the dorsal surface of the carapace, near its anterior border, are the *paired eyes* (*E*), closely approximated in front, diverging posteriorly. Immediately in front of them is a small black *median eye* (*e.*), and between their diverging posterior ends a semi-transparent oval area, the *dorsal organ*

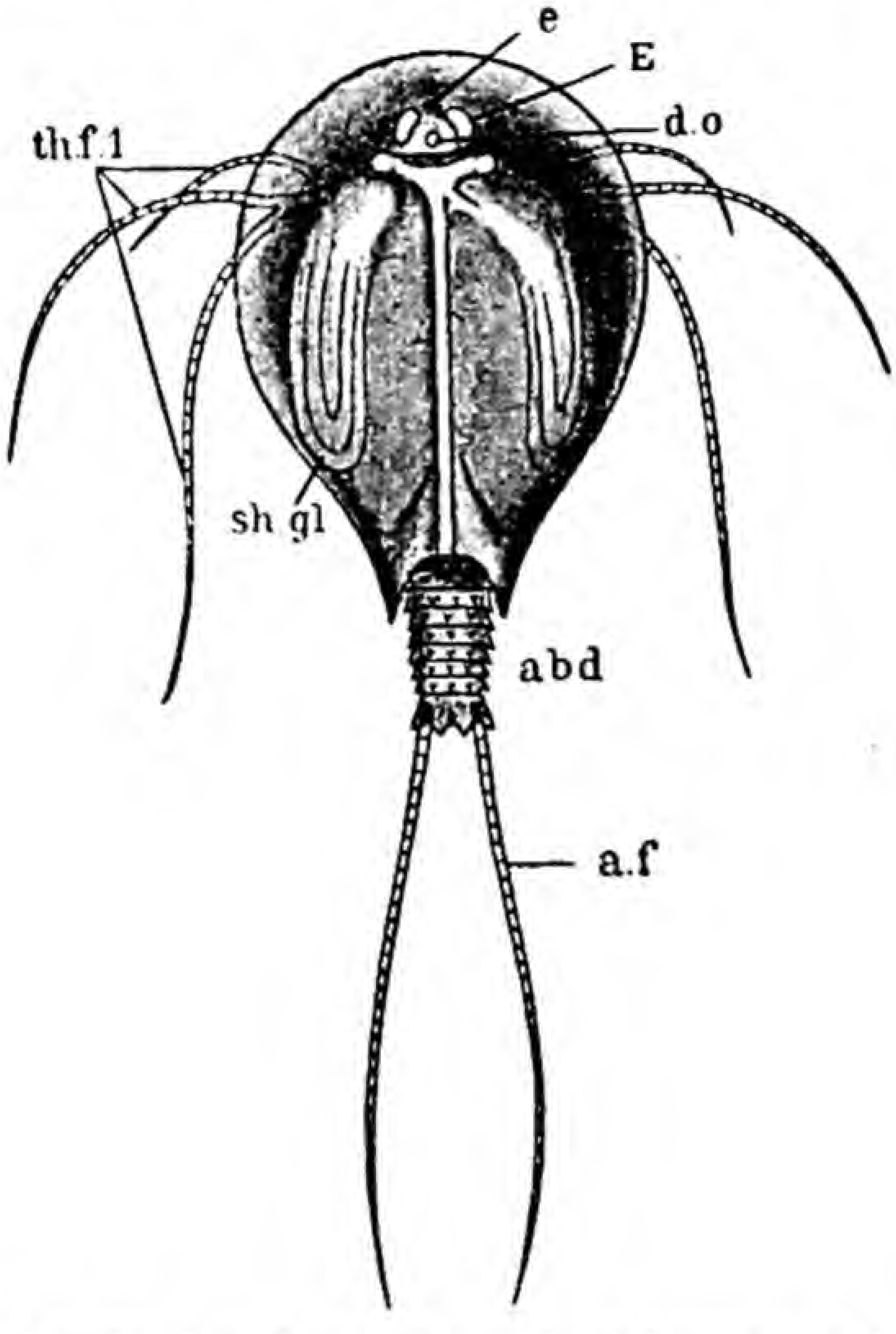


FIG. 353.—**Apus cancriformis,** dorsal aspect. *abd.* abdomen; *a. f.* caudal styles; *d. o.* dorsal organ; *E.* paired eye; *e.* median eye; *sh. gl.* shell-gland; *th. f. 1*, endites of first thoracic foot. (From Bronn's *Tierreich.*)

(*d. o.*). Passing transversely across the carapace, a short distance behind the dorsal organ, is a shallow furrow, the *cervical fold*, immediately posterior to which a pair of coiled tubes (*sh. gl.*) are seen, one on each side of the carapace: these are the *shell-glands* or excretory organs.

The carapace is attached only as far back as the cervical fold: behind that level it is free, and, when lifted up or cut away (Fig. 354), shows the greater part of the body of the animal, divided into segments like the posterior portion. From the cervical groove backwards about twenty-eight or thirty segments can be counted: the region in front of the cervical groove shows no signs of segmentation, and is distinguished as the *head*. The segments have the form of

chitinous rings, often produced into small spines: each ring slightly overlaps its successor, and is connected with it by a narrow area, the *articular membrane*,

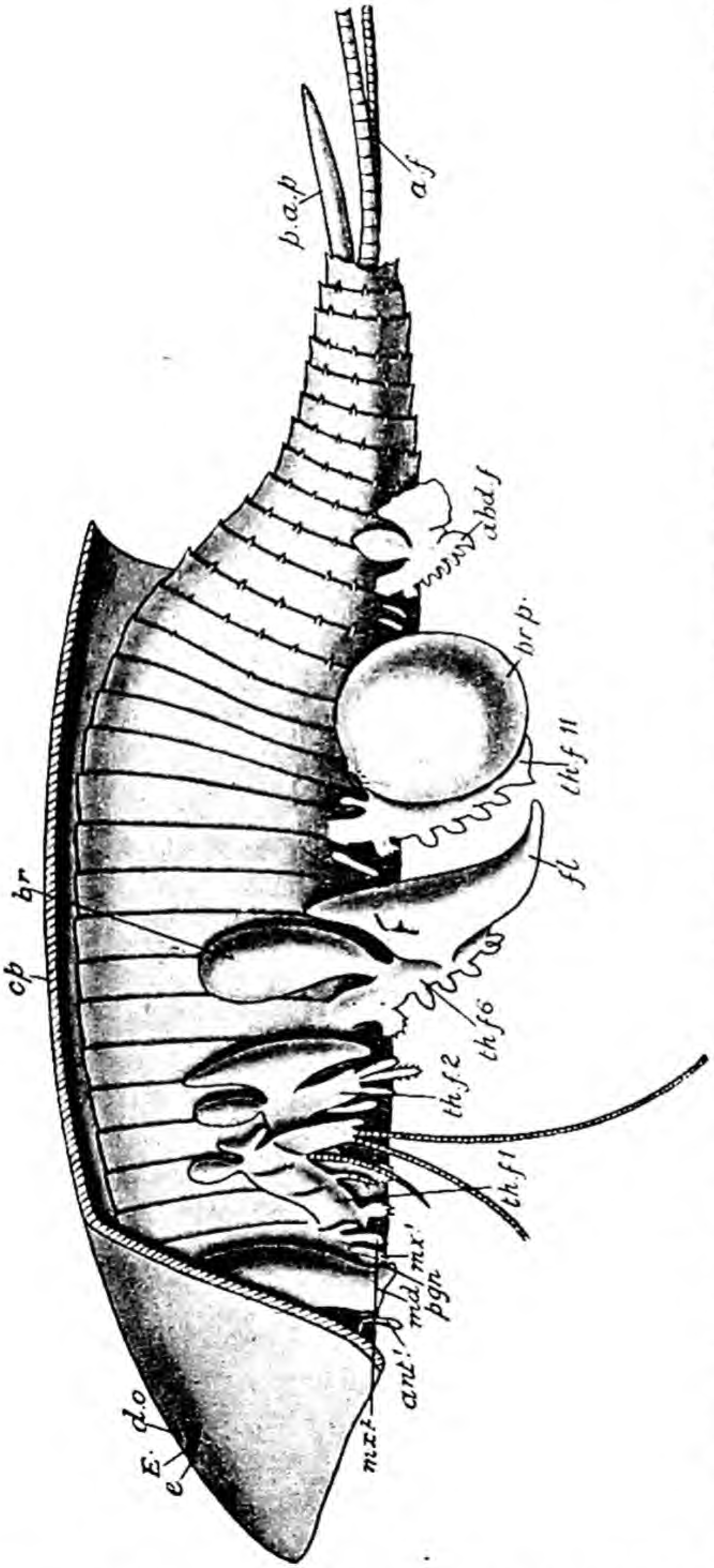


FIG. 354.—**Lepidurus kirkii,** side view, with half of carapace and most of the appendages removed. *a. f.* caudal styles; *abd. f.* abdominal foot; *ant. 1*, antennule; *br.* bract; *br. p.* brood-pouch; *cp.* carapace; *d. o.* dorsal organ; *E.* paired eye; *e.* median eye; *fl.* flabellum; *md.* mandible; *mx. 1*, *mx. 2*, maxillæ; *p. a. p.* post-anal plate; *pgn.* paragnatha; *th. f. 1*—*th. f. 11*, thoracic feet.

the chitinization of which is less pronounced than that of the rings themselves. By this arrangement the segments are freely movable upon one another in all

directions, the articular membranes acting as joints. The last or anal segment is pierced by the terminal *anus* (Fig. 358, *an.*).

The ventral surface of the head is formed by a flattened *sub-frontal plate* (Fig. 355, *s.f.pl.*), continuous marginally with the carapace. The posterior edge of this plate is convex backwards, and is produced in the middle line into a shield-shaped process, the *labrum* or upper lip (Figs. 355, *lbr.*, 356, L), which overhangs the *mouth*. From the sub-frontal plate also arise, on each side, two delicate processes, the innermost called the *antennule* (Figs. 355, *ant.* 1; 356 *a'*.), the outermost the *antenna* (*ant.* 2; *a''*.): these are the first two pairs of *appendages*. The third pair consists of two strong toothed bodies of a deep brown colour, placed one on each side of the mouth, and called the *mandibles* (*md.*). The remaining appendages form two rows of delicate leaf-like processes, attached to the segmented portions of the body, and overlapping one another from before backwards: their number varies from forty to nearly seventy (*th. f.*, *abd. f.*).

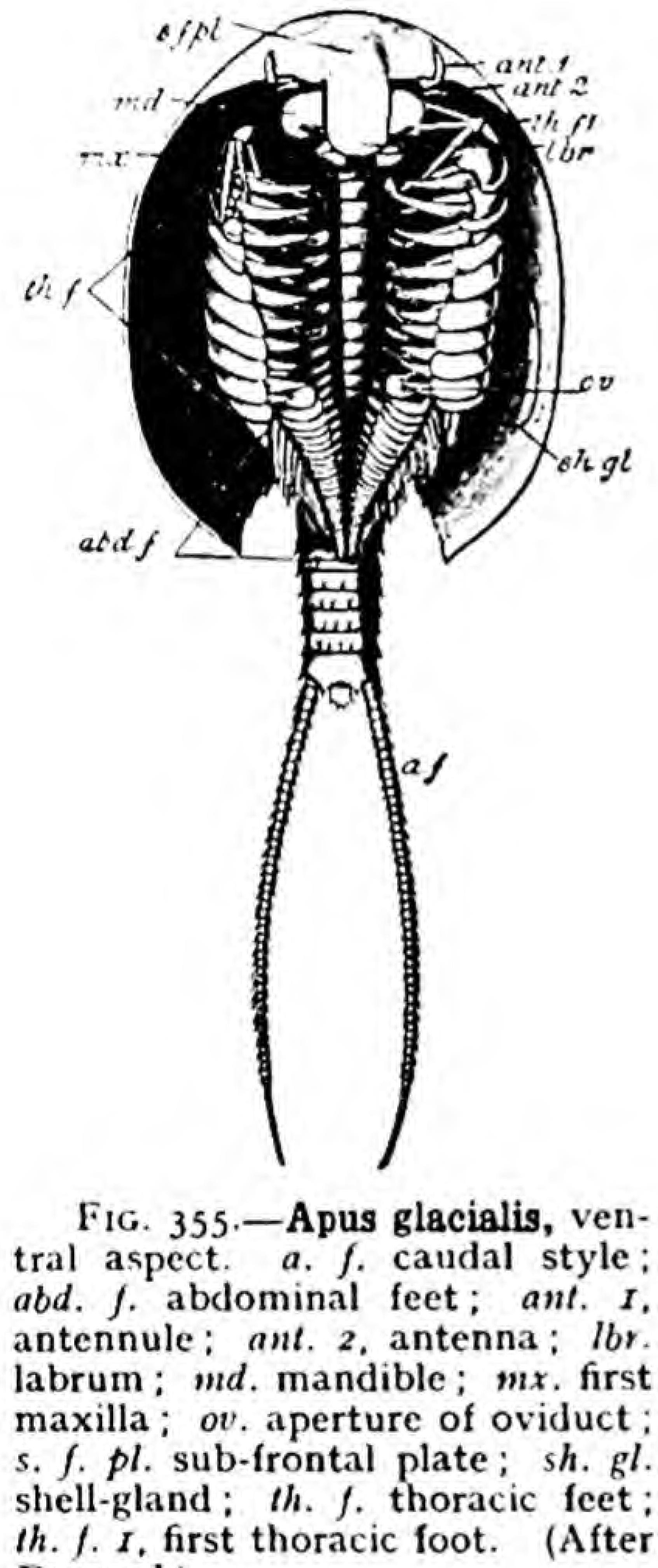


FIG. 355.—**Apus glacialis,** ventral aspect. *a. f.* caudal style; *abd. f.* abdominal feet; *ant. 1*, antennule; *ant. 2*, antenna; *lbr.* labrum; *md.* mandible; *mx.* first maxilla; *ov.* aperture of oviduct; *s. f. pl.* sub-frontal plate; *sh. gl.* shell-gland; *th. f.* thoracic feet; *th. f. 1*, first thoracic foot. (After Bernard.)

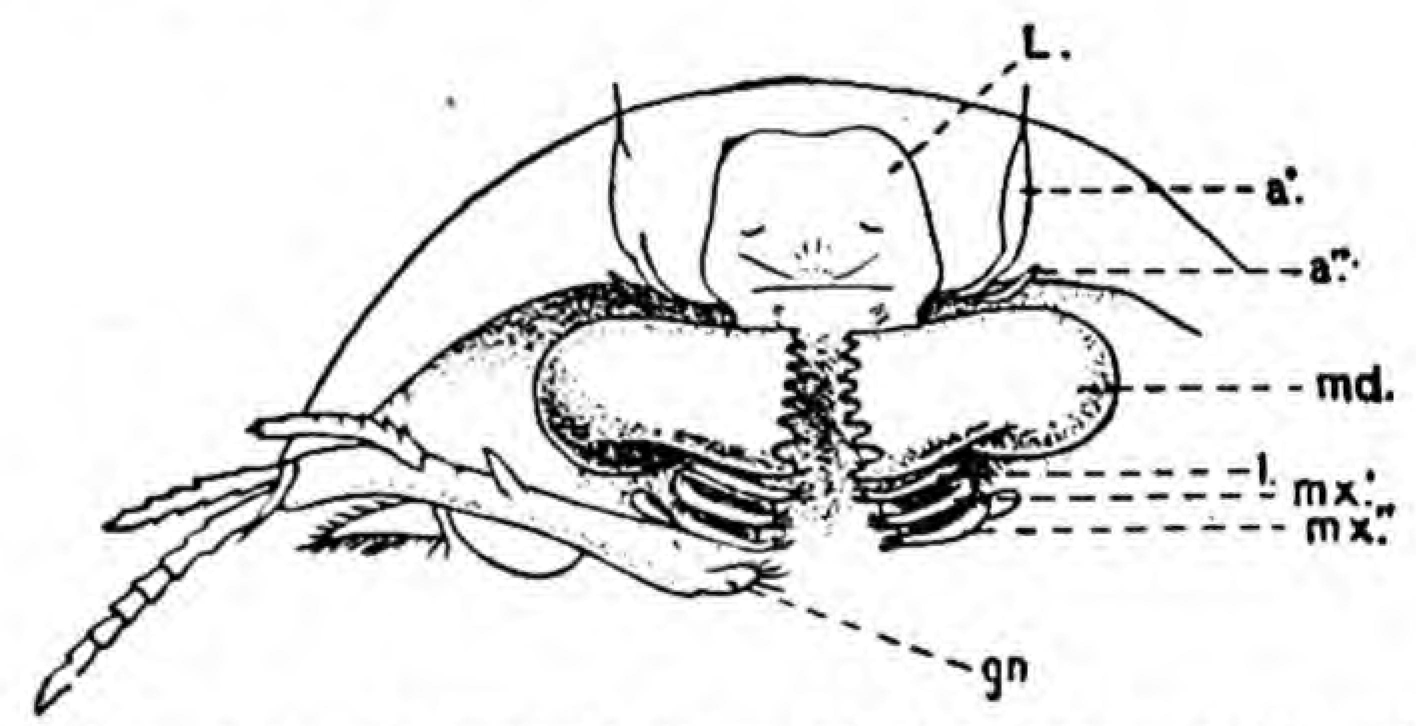


FIG. 356.—A ventral view of the head region of **Lepidurus glacialis.** *a'*. antennule; *a''*. antenna; *gn.* gnathobase; *L.* labrum (turned forwards); *l.* paragnathum; *md.* mandible; *mx'*. first maxilla; *mx''*. second maxilla. (From Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge) after Calman.)

Appendages.—The *antennule* (Fig. 357, *1*) consists of a bent rod bearing delicate chitinous bristles or *setæ* at its tip, and presenting, at the bend, a joint, due to the presence of an articular membrane. The appendage is thus made up of two *podomeres* or limb-segments, movably articulated together. Its function is probably tactile.

The *antenna* (*2*) is absent in some species both of Apus and Lepidurus: in *A. cancriformis* it is a very delicate hook-shaped unjointed structure,

probably functionless. As we shall see from the study of development, it is a vestigial organ.

The *mandible* (3) is also an unjointed appendage. It has the form of a deeply concavo-convex plate, strongly chitinized, and produced along its inner edge into strong teeth. The mandibles lie one on each side of the mouth, and are so articulated that, by means of muscles, their toothed edges can be brought together in the middle line, so as to rend the food.

The fourth and fifth appendages are very small, and are probably functionless or nearly so: they follow one another just behind the mandible, and are called the *first* and *second maxillæ*. The first maxilla (4) consists of two curved

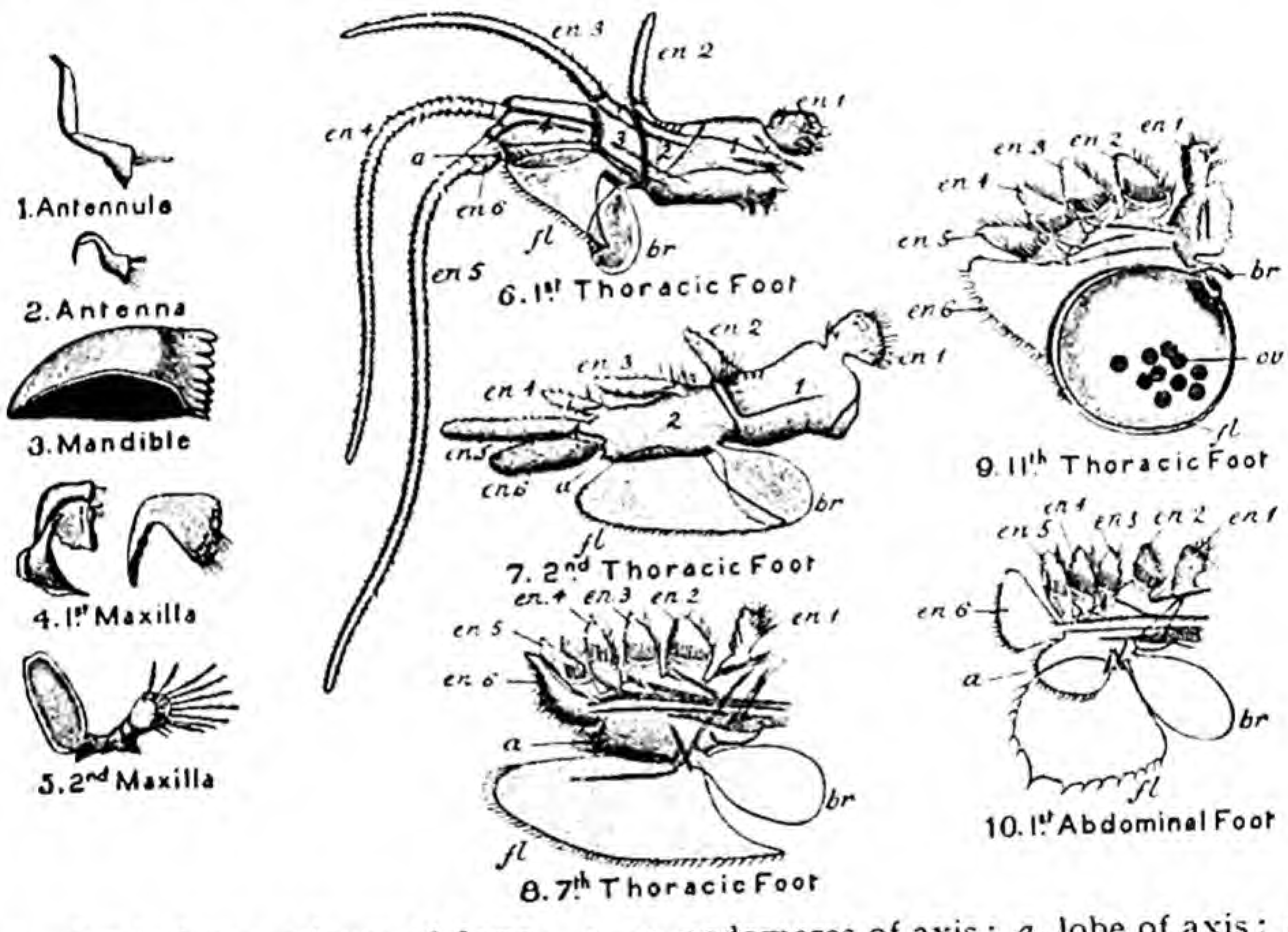


FIG. 357.—Typical appendages of **Apus.** *1—4*, podomeres of axis; *a.* lobe of axis; *br.* bract; *en. 1—en. 6*, endites; *fl.* flabellum; *ov.* ova. (After Lankester.)

chitinous plates, the second of a basal portion produced into two branches (5). Between the first maxilla and the mandibles are a pair of delicate unjointed processes, the *paragnatha* (Figs. 354, *pgn.*; 356, *l.*): they form together a sort of lower lip, and are not usually reckoned as appendages.

The foregoing appendages all spring from the unsegmented anterior portion of the body or head. As we shall see, however, the succeeding limbs arise each pair from its own segment, so that the presence of five pairs of appendages on the head may be taken provisionally as an indication that this region of the body is composed of five fused segments.

The sixth appendage (6) springs from the ventro-lateral region of the first clearly marked segment, and is the first of the long row of appendages plainly visible in a ventral view. It consists of an *axis* formed of four podomeres

(*1–4*), and bearing a number of offshoots: six of these, called *endites* (*en. 1—en. 6*), arise from its inner or mesial border; two, called *exites* (*br.*, *fl.*), from its outer or lateral border. The proximal endite (*en. 1*) is small, and bears strong spines; in connection with its fellow of the opposite side it is used to seize food-particles and pass them on to the mouth: it is therefore conveniently distinguished as the *gnathobase*. The distal endite is rudimentary (*en. 6*): the remaining four (*en. 2–5*) are long, jointed filaments. The distal exite is nearly triangular, and is called the *flabellum* (*fl.*); the proximal exite is oval, and is known as the *bract* or branchia (*br.*); both probably serve a respiratory function.

The seventh appendage (*7*) has only two podomeres in the axis, and the endites are comparatively short and flat. The next eight, *i.e.* those borne on the third to the tenth free segments, closely resemble one another: each (*8*) has an unjointed axis and short leaf-like endites, the whole appendage having a distinctly foliaceous character. The sixteenth appendage—that of the eleventh free segment—resembles its predecessors in the male, but in the female (*9*) is peculiarly modified. The distal portion of the axis forms a hemispherical cup, over which the flabellum (*fl.*) fits like a lid: in this way a capsule or *brood-pouch* is produced, which serves for the reception of the eggs, and the appendage is distinguished as the *oostegopod* or brood-foot. The brood-feet and the adjacent genital apertures allow of a very convenient division of the body: all that region from the first free or postcephalic segment to that bearing the oostegopods, both inclusive, is called the *thorax*, and its appendages the *thoracic feet*: it consists of eleven metameres. The remaining segments, from the twelfth to the last inclusive, constitute the *abdomen*, and their appendages are called the *abdominal feet*.

The abdominal resemble the thoracic feet in general characters, having the same foliaceous form (*10*), with unjointed axis, small leaf-like endites, and large flabellum and bract. They gradually diminish in size from before backwards; and, from the third abdominal segment onwards, two or more pairs of appendages spring from each segment, so that while the total number of abdominal segments, in *A. cancriformis*, is twenty-two, and the five hindermost of these are without appendages, there are altogether fifty-two pairs of abdominal feet. It seems probable that segments bearing more than one pair of appendages represent two or more fused—or, perhaps one should rather say, imperfectly differentiated—metameres.

Body-wall.—The whole body is, as already mentioned, covered by a layer of chitin of varying thickness, which constitutes an *exoskeleton* or external supporting structure. Immediately underlying it is the deric epithelium or epidermis, from which the chitin is secreted layer by layer. Thus the exoskeleton of Apus is a continuous cuticular structure, exhibiting segmentation in virtue of the fact that, while comparatively thick and strong in places where no move-

ment is required, it is thin and flexible in the intervening spaces, and thus allows of the movement of the harder parts upon one another.

The setæ, which occur on many parts of the body, and in particular fringe the appendages, are hollow offshoots of the chitinous cuticle, containing a protoplasmic core continuous with the epidermis. They thus differ fundamentally from the setæ of Chætopods, which are solid rods sunk in muscular sacs.

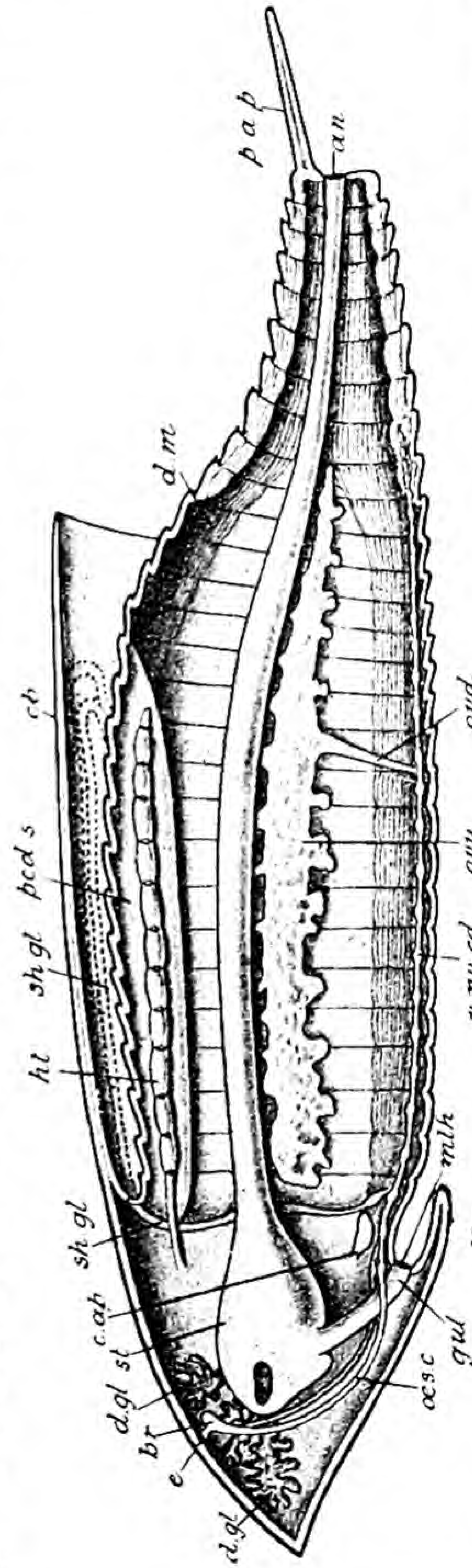


FIG. 358.—**Lepidurus kirkii**, sagittal section (semi-diagrammatic). *an.* anus; *br.* brain; *c. ap.* cephalic apodeme; *cb.* carapace; *d. gl.* digestive gland; *d. m.* dorsal muscles; *e.* median eye; *gul.* gullet; *ht.* heart; *lbr.* labrum; *mth.* mouth; *œs. c.* œsophageal connective; *ovd.* oviduct; *ovy.* ovary; *p. a. p.* post-anal plate; *pcd. s.* pericardial sinus; *sh. gl.* shell-gland; *st.* stomach; *v. nv. cd.* ventral nerve-cord.

The **muscular system** is well developed (Figs 358, 359). Underlying the epidermis is a layer of connective-tissue, and beneath this is found, in the posterior or limbless part of the abdomen, a layer of longitudinal muscles encircling the body and attached by connective-tissue to each segment. In this way the muscular layer is itself segmented, being divided by the connective tissue insertions into muscle-segments or *myomeres*. The action of these muscles is to approximate adjacent segments: according as the fibres on the dorsal, ventral, or lateral regions contract, the abdomen will be raised, lowered, or turned sideways. In the limb-bearing portion of the abdomen and in the thorax there is no longer a continuous muscular tube, but paired dorsal (*d.m.*) and ventral bands, which pass respectively above and below the origins of the limbs: the dorsal bands arise in front from the head-region, the ventral from a strong fibrous plate, the *cephalic apodeme* (*c. ap.*), lying just behind the gullet.

Each appendage is moved as a whole by muscles passing into it from the trunk: its various parts are acted upon by delicate muscular slips running to the various podomeres of the axis and to the endites, thus rendering them

separately movable. The only example we have yet met with of appendages moved by definite muscular bands is that of the curious Rotifer *Pedalion*. The muscles are all striped, a character which applies to the Arthropoda generally.

Digestive Organs.—The *mouth* (Fig. 358, *mth.*) is situated on the ventral surface of the head, and is bounded in front by the labrum (*lbr.*), on each side by the mandibles, and behind by the paragnatha. The food appears to be pushed forwards towards the mouth by the toothed bases of the thoracic feet, and is broken up by the mandibles, which work laterally. The maxillæ are probably functionless, or nearly so.

The mouth leads into a narrow *gullet* (*gul.*), which passes upwards and forwards into the head and enters a wide *stomach* (*st.*), from which a straight *intestine* (*int.*) is continued back to the terminal anus (*an.*). From each side of the stomach is given off a wide tube (*d.gl.*) which branches extensively, its ramifications finally ending in delicate cæca. The larger branches of these *digestive glands* contain food in process of digestion: their ultimate cæca secrete a digestive juice: the walls of the stomach itself are non-glandular. The walls of the enteric canal consists of an inner layer of epithelium and an outer layer of connective-tissue and muscle. In the gullet and in the posterior end of the intestine the epithelium secretes a thin cuticle, which thus comes to form the actual lining of the cavity. It is shown by development that the portion of the canal devoid of a chitinous lining is formed from the archenteron of the embryo: the gullet is developed from the stomodæum, the posterior end of the intestine from the proctodæum.

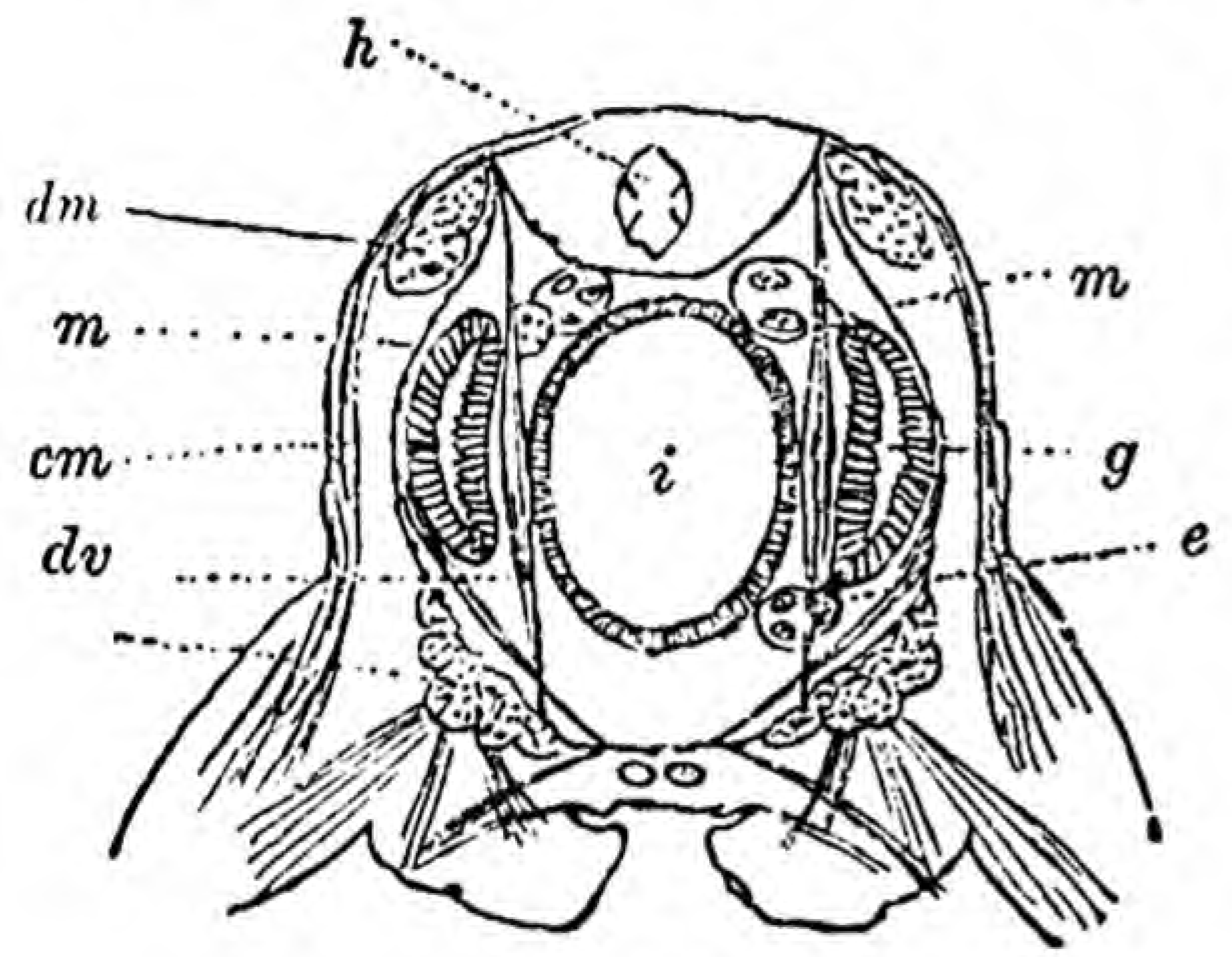


FIG. 359.—Transverse section of **Apus.** *cm.* muscles to feet; *dv.* dorso-ventral muscles; *e.* eggs; *dm.* dorsal muscles; *g.* ovary; *h.* heart; *i.* intestine; *m.* partition between intestinal and lateral sinus; *vm.* ventral muscles. (From Bernard.)

The **body-cavity** is divided into several parts by membranous partitions (Fig. 359): there is a large median cavity in which the enteric canal (*i*) lies, called the *intestinal sinus*: on each side of this are *lateral sinuses* containing the muscles; and in the dorsal region is a median cavity, the *pericardial sinus*. All these spaces are devoid of an epithelial lining, and contain blood: as will become evident later, they do not correspond with the cœlome of the higher worms.

The central organ of the **circulatory system** is the *heart* (Fig. 358, *ht.*, and

Fig. 359, *h.*), a narrow tube contained in the pericardial sinus. It is pierced laterally by several pairs of apertures or *ostia* provided with valves opening inwards, and is continued in front into a narrow tube, the *cephalic artery* (*c. art.*), which extends into the head and gives off near its origin a pair of arteries to the shell-glands (Fig. 355). When the heart contracts, the blood is driven through these arteries to the head and carapace: it then travels backwards in the intestinal sinus, passes to the limbs, and is returned to the pericardial sinus, finally re-entering the heart, during its diastole, through the ostia. The plasma of the blood is coloured red by hæmoglobin, and contains amœboid corpuscles.

As already mentioned, the function of **respiration** is discharged by the flabella and bracts of the feet, which are abundantly

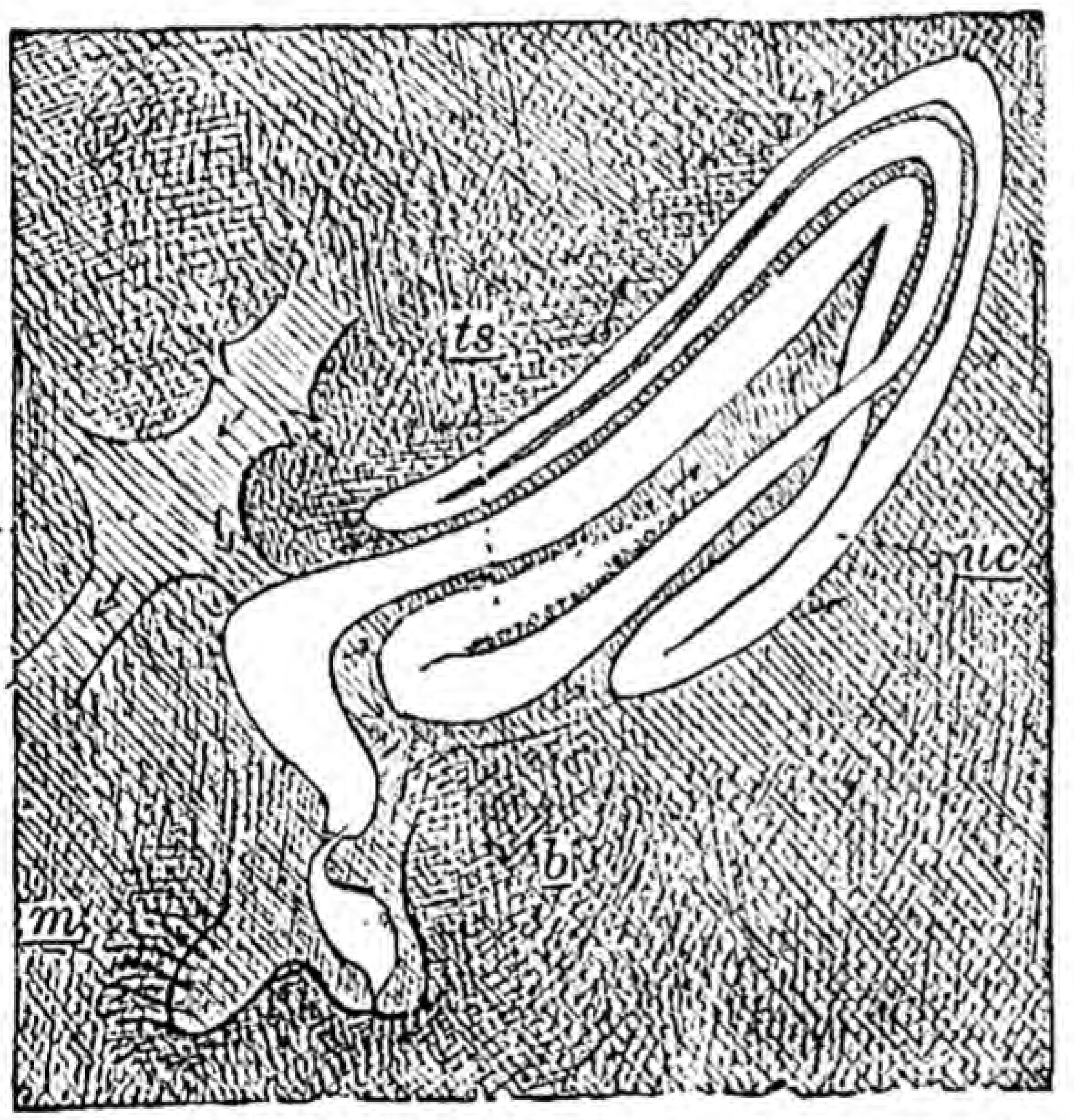


FIG. 360.—Shell-gland of **Apus**, diagrammatic. *ac.* cephalic artery; *b.* bladder; *h.* heart; *m.* second maxilla; *t. s.* end-sac; *uc.* urinary tube. (From Bernard.)

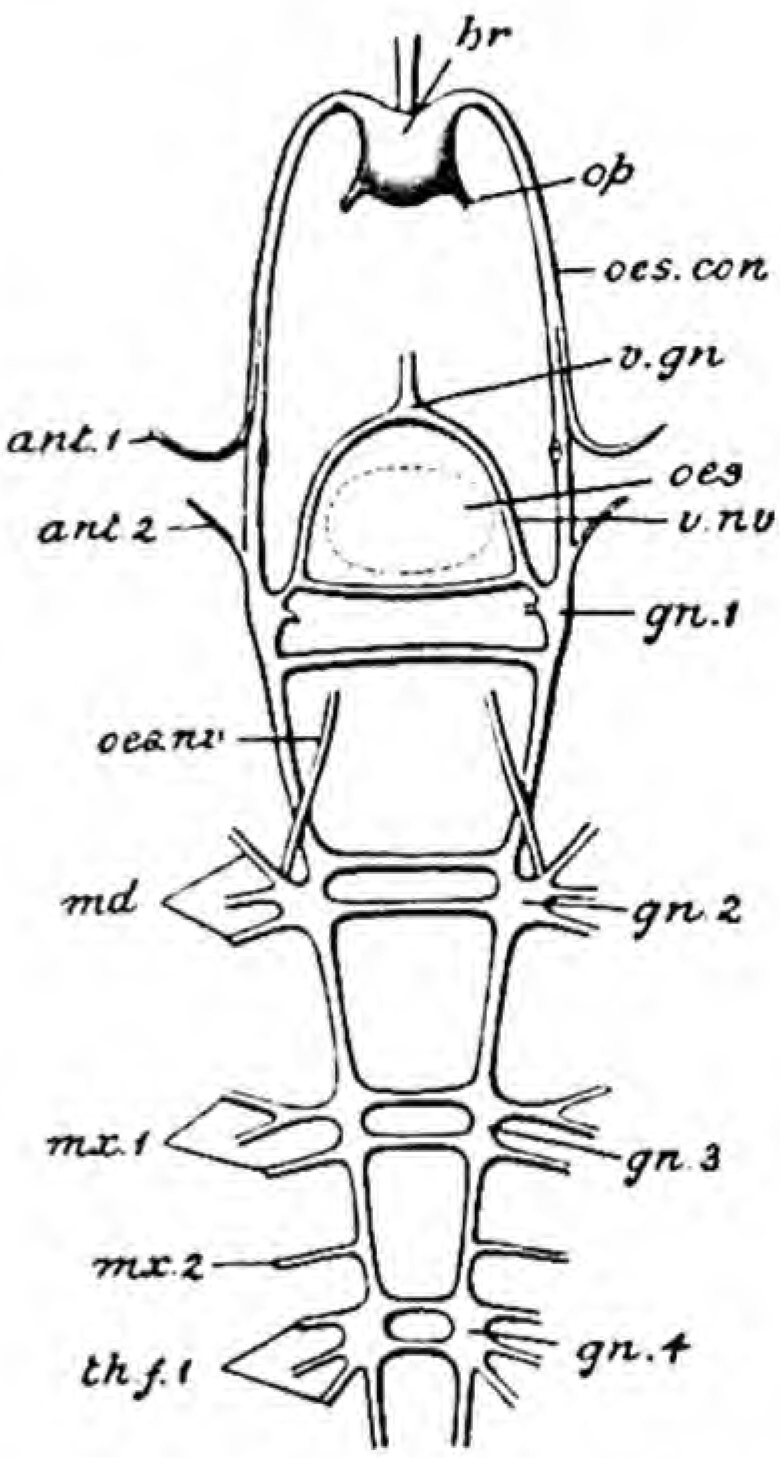


FIG. 361.—Nervous system of **Apus cancriformis.** *ant. 1* nerve to antennule; *ant. 2* to antenna; *br.* brain; *gn. 1—4*, first four ganglia of ventral nerve-cord; *md.* mandibular nerve; *mx. 1*, nerve of first maxilla; *mx. 2*, of second maxilla; *œs. con.*, œsophageal connective; *op.* optic nerve; *th. f. 1*, nerve of first thoracic foot; *v. gn.* visceral ganglion; *v. nv.* visceral nerve. (After Lankester and Pelseneer.)

supplied with blood and the movements of which ensure a constant renewal of the water in their neighbourhood. The **renal organ** or *shell-gland* (Fig. 360) consists of a coiled *urinary tube* (*uc.*) lying between the two layers of the carapace and lined by gland-cells. At one end the tube is connected with an *end-sac* (*ts.*), also lined with glandular epithelium; at the other it dilates into a small *bladder* (*b.*) which opens on the second maxilla (*m.*).

The **nervous system** (Fig. 361) is constructed on the annelidan type. There

is a squarish *brain* (*br.*) situated in the dorsal region of the head, beneath the eyes. From it a pair of *œsophageal connectives* pass backwards and downwards to join the *ventral nerve-cord*, which consists of a double chain of ganglia (*gn. 1–4*) united by longitudinal connectives and transverse commissures so as to have a ladder-like appearance. The first pair of ganglia lies immediately behind the mouth, and sends off *visceral nerves* which join to form a ring round the gullet, swollen in front into a small *visceral ganglion* (*v. gn.*). Passing backwards the nerve-chain diminishes in size, and comes to an end at about the level of the last pair of abdominal feet (Fig. 358).

The origin of the nerves given off from the central nervous system presents many points of interest. From the fourth ganglion of the ventral cord backwards each pair of appendages has its own pair of ganglia, the metameric correspondence between the limbs and the nervous system being complete. The mandibles and the first maxillæ also receive nerves, each from their own pair of ganglia, their serial homology with the more typical appendages being thus confirmed. But the second maxillæ receive their nerves (*mx. 2*) from the connectives between the third and fourth ganglia: the ganglion belonging to their segment may be assumed to have atrophied. The antenna is supplied by a nerve (*ant. 2*) which springs from the œsophageal connective, but which can be traced backwards to the first ganglion of the ventral chain: this fact may be taken as an indication that the antennæ are serially homologous with the jaws and feet—that they are, in fact, metameric or post-oral appendages which have shifted forwards, one on each side of the mouth, thus becoming pre-oral. The nerve of the antennule (*ant. 1*) also springs from the œsophageal connective, but is traceable forwards to the brain, where it is connected with a special group of nerve-cells. This has been explained by supposing that the antennule is a post-oral appendage the ganglion of which has moved forwards along the œsophageal connective and fused with the brain—a process which actually takes place with the ganglia of the antennæ in the higher Crustacea. The median and paired eyes are supplied by nerves from the brain.

Sense-organs.—The setæ which occur on so many parts of the body, and especially as fringes to the limbs, are to be considered as *organs of touch*: the only other sense-organs are the eyes. The *paired eyes* are, as we have seen, situated on the dorsal surface of the head, just over the brain: they are covered by a transparent cuticle forming the *cornea*, beneath which is a narrow space or *water-sac*, communicating with the exterior by a pore, and therefore filled with water. The eye itself is made up of a large number of radially arranged elements called *ommatidia* (Fig. 362), each of which consists of an outer and an inner portion. The outer portion is a group of clear glassy cells (*cc.*) enclosing a transparent homogeneous *vitreous body* (*cr.*): the whole of this portion of the eye serves as a dioptric apparatus, like our own lens and vitreous humour. The inner portion is a group of sensory cells, constituting a *retinula* (*rc.*), and

enclosing a refractive rod, the *rhabdome* (*rh.*): the retinula is the actual percipient part of the ommatidium, its cells being comparable to our own rods and cones. The retinulæ of adjacent ommatidia are separated from one another by cells full of black pigment (*p.*), so that each ommatidium is in a state of optical isolation from its fellows, and the whole eye is what is called a *compound eye*. The optic nerve springing from the brain dilates into an *optic ganglion*, from which fibres pass to the retinulæ.

The *median eye* is an ovoid body, and consists of four groups of large sensory

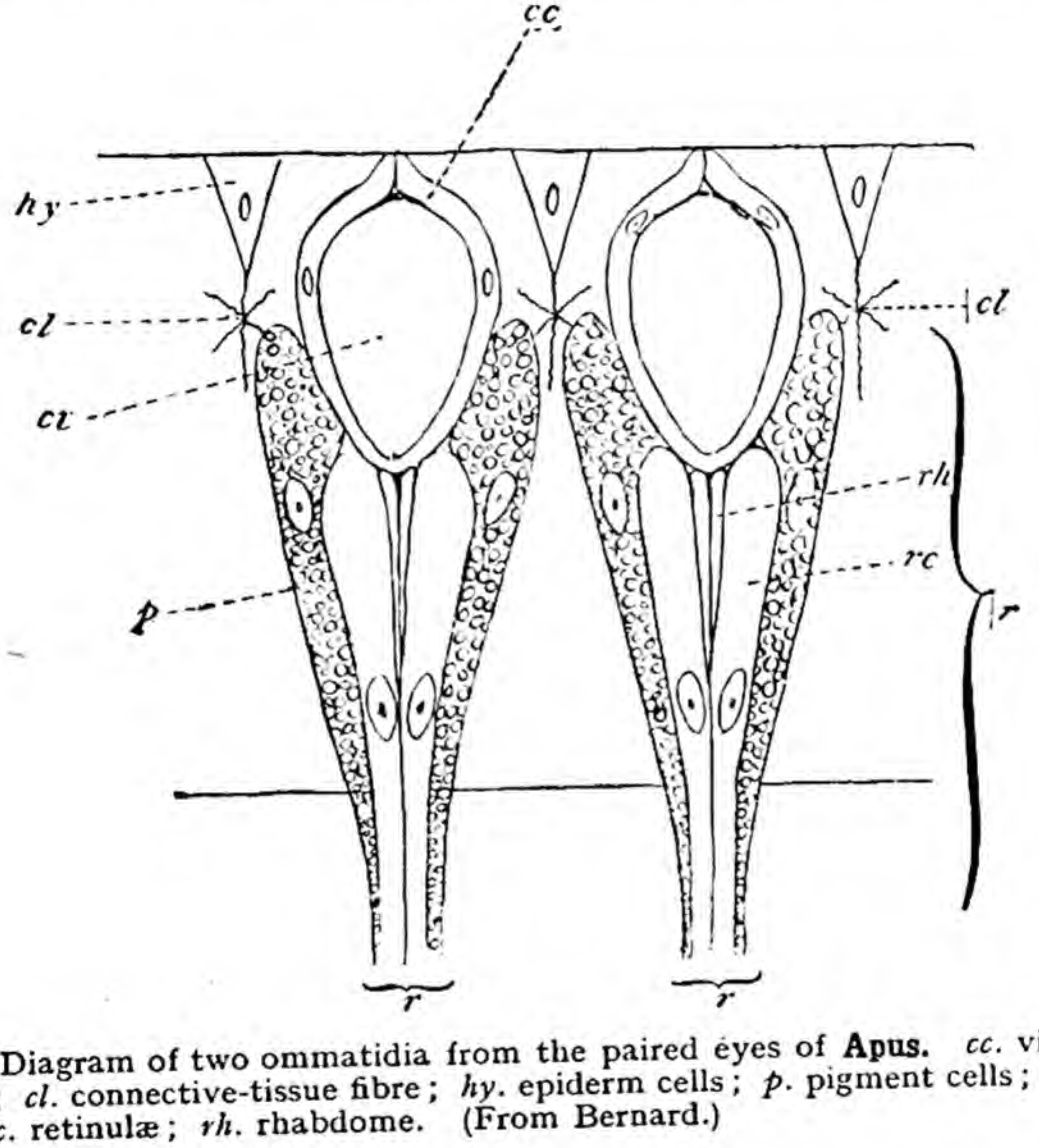


FIG. 362.—Diagram of two ommatidia from the paired eyes of **Apus.** *cc.* vitreous cells; *cr.* vitreous body; *cl.* connective-tissue fibre; *hy.* epiderm cells; *p.* pigment cells; *r.* inner parts of ommatidia; *rc.* retinulæ; *rh.* rhabdome. (From Bernard.)

cells enclosing a mass of pigmented tissue: it is in immediate contact with the brain, and receives a narrow canal from the water-sac beneath the cuticle of the paired eyes.

Reproductive Organs.—The large majority of individuals both of Apus and Lepidurus are females; males are of comparatively rare occurrence. The *ovary* (Fig. 358, *ovy.*) is a branched tube occupying a considerable portion of the body-cavity in sexually mature individuals. The walls of the tube are lined with epithelium, and give rise to ova, which pass into the lumen of the tube and thence to a duct (*ovd.*) opening on the eleventh or last thoracic segment. As in Leeches (p. 363), there is reason for thinking that the cavity of the ovarian tube

represents a shut-off portion of the cœlome, and the oviduct a cœlomoduct. One species has been shown to be hermaphrodite: in others males are occasionally found, but reproduction appears to be, as a rule, parthenogenetic.

Development.—The eggs are *centrolecithal, i.e.* have an accumulation of yolk in the centre surrounded by a superficial layer of protoplasm.

The embryo is hatched in the form shown in Fig. 363, *A*. The body is

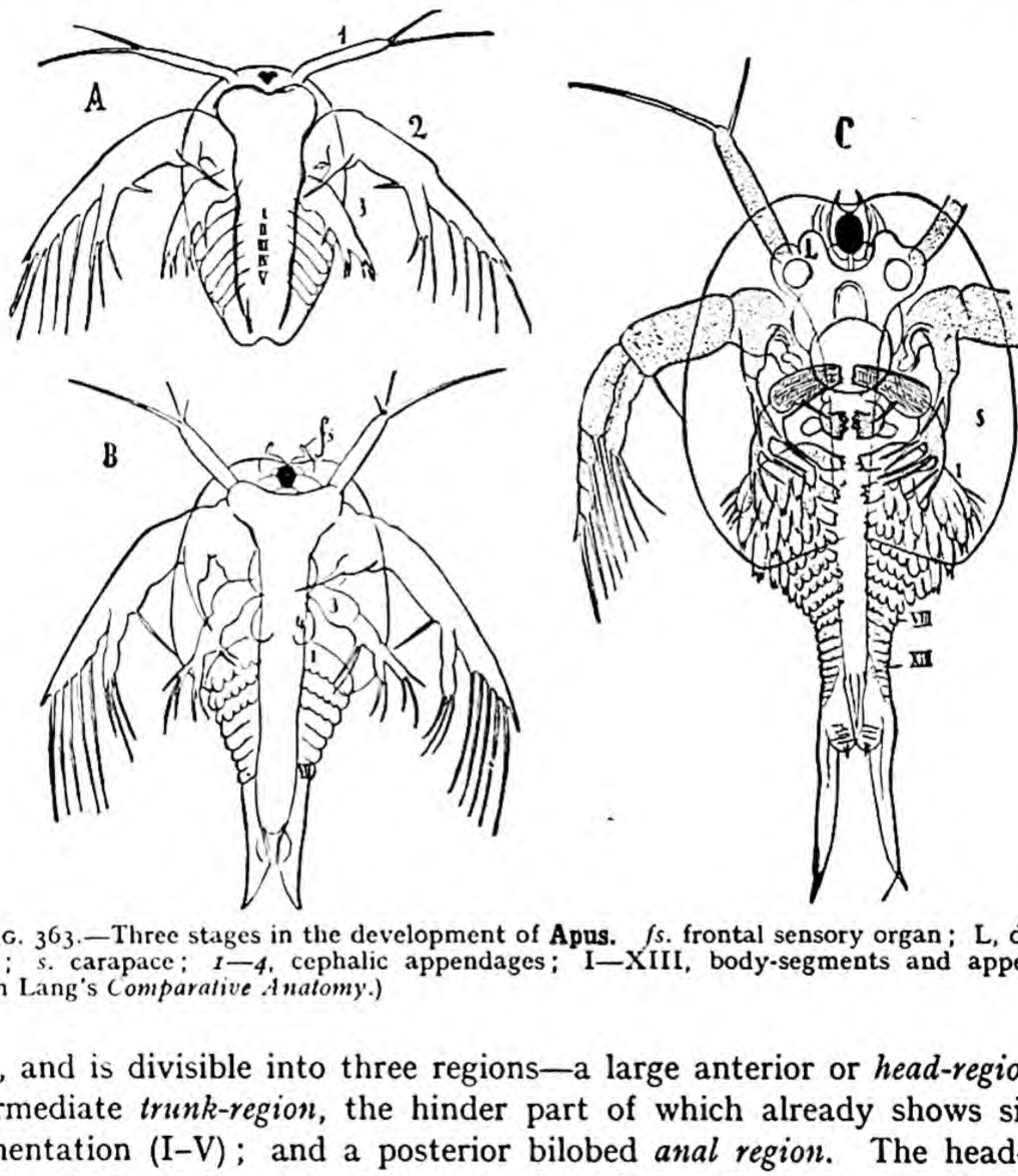


FIG. 363.—Three stages in the development of **Apus.** *fs.* frontal sensory organ; L, digestive gland; *s.* carapace; *1—4*, cephalic appendages; I—XIII, body-segments and appendages. (From Lang's *Comparative Anatomy*.)

oval, and is divisible into three regions—a large anterior or *head-region*; an intermediate *trunk-region*, the hinder part of which already shows signs of segmentation (I–V); and a posterior bilobed *anal region*. The head-region bears a single median eye, and a pair of small unjointed appendages (*1*), each with two large setæ at its extremity: these become the antennules of the adult. The trunk-region bears two pairs of appendages, the first of which (*2*) is very large and fringed with setæ, but is chiefly remarkable for being *biramous* or two-branched—being formed of a proximal portion or stem, the *protopodite*; a small inner branch, the *endopodite*; and a large outer branch, the *exopodite*. This second appendage becomes the antenna of the adult, and may be called the

antennary foot: it is the chief organ of locomotion of the larva. The second-trunk appendage is the *mandibular foot* (*3*), so called because it becomes converted into the mandible of the adult: it is also biramous. The only internal structure to be noted is the straight enteric canal with its dilated anterior end or stomach: the mouth opens between the bases of the antennary and mandibular feet, and is bounded in front by a large labrum: the anus is at the extremity of the anal region. This very peculiar and characteristic larval form is called a *nauplius*.[1]

The nauplius swims freely, chiefly by vigorous strokes of the great antennary feet, and after a time undergoes a series of moults or *ecdyses*, the cuticle being cast off and the animal emerging in the form shown in Fig. 363, *B*. The trunk-region has elongated, new segments having been added, as in Chætopods, between those previously present and the anal region. The antennules have become shifted backwards, and rudiments of a fourth pair of appendages, the first maxillæ (*4*), have appeared. The carapace has grown out from the dorsal region of the head, and a peculiar paired sense-organ (*f.s.*) has appeared on the head.

After two more ecdyses the larva has assumed the form shown in Fig. 363, *C*. Several new segments have been added, and the anterior of these all bear leaf-like thoracic feet. The antennary feet are still very large, and the bases of the mandibular feet have become enlarged and toothed so as to form biting jaws. The carapace (*s.*) has increased greatly, and the caudal styles have attained a considerable size. Further moults occur, new segments are added with their appendages, the antennules and antennæ degenerate—the latter sometimes disappearing altogether, the mandibles become reduced to the enlarged basal segment, and the larva passes by almost insensible gradations into the adult form.

b. The Fresh-water Crayfish (*Astacus* (*Potamobius*) *fluviatilis*).

Astacus fluviatilis is common in streams and rivers in England and the continent of Europe; allied species occur in Asia and North America; and fresh-water Crayfishes belonging to other genera, but agreeing with Astacus in all essential features, are found in America, Australia, and New Zealand.

External Characters.—The body of the Crayfish (Fig. 364) is divided into two regions—an anterior, the *cephalothorax*, which is unjointed, and is covered by a *carapace* (*c.*), resembling that of Apus, but of smaller proportional size; and a posterior, the *abdomen* (*abd.*), which is divided into distinct segments, movable upon one another in a vertical plane. The cephalothorax is again divided into two regions—an anterior, the *head*; and a posterior, the *thorax*—by a transverse depression, the *cervical groove* (*c.v.g.*). The divisions of the

[1] More strictly *metanauplius*: the typical nauplius exhibits no segmentation of the trunk-region.

body are thus the same as in Apus, but the abdomen alone is movably segmented, owing to the fact that the carapace, instead of being a purely cephalic structure continued backwards as a loose fold over the thorax, is developed

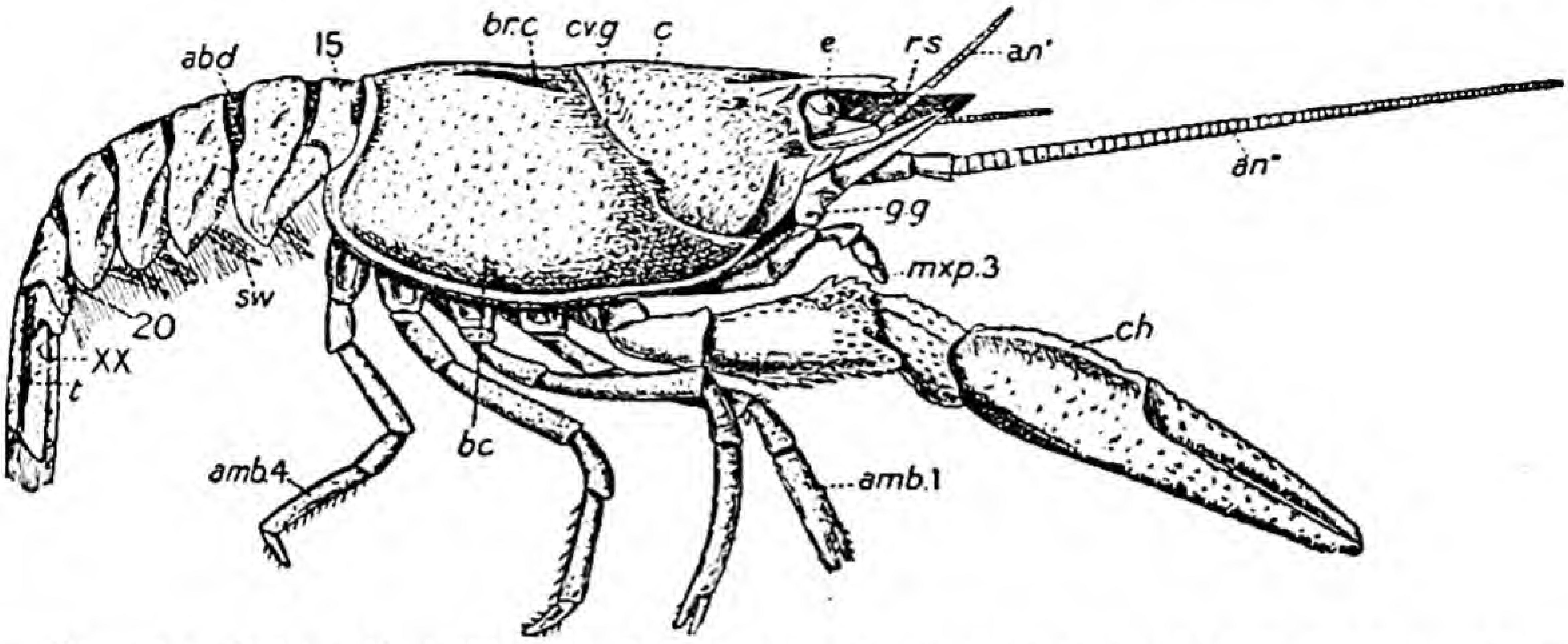


FIG. 364.—**Astacus fluviatilis,** lateral view. *abd.* abdomen; *amb. 1*, first walking leg; *amb. 4.*, fourth walking leg; *an'.* antennule; *an''.* antenna; *bc.* branchiostegite; *br. c.* branchiocardiac groove; *c.* carapace; *ch.* chela; *cv. g.* cervical groove; *e.* eye; *g. g.* opening of green glanid; *mxp.* 3, third maxilliped; *rs.* rostrum; *sw.* swimmeret or pleopod; *t.* telson; 15. first segment of abdomen; 20. last segment of abdomen; XX. uropod. (From Shipley and MacBride's *Zoology* (University Press, Cambridge).)

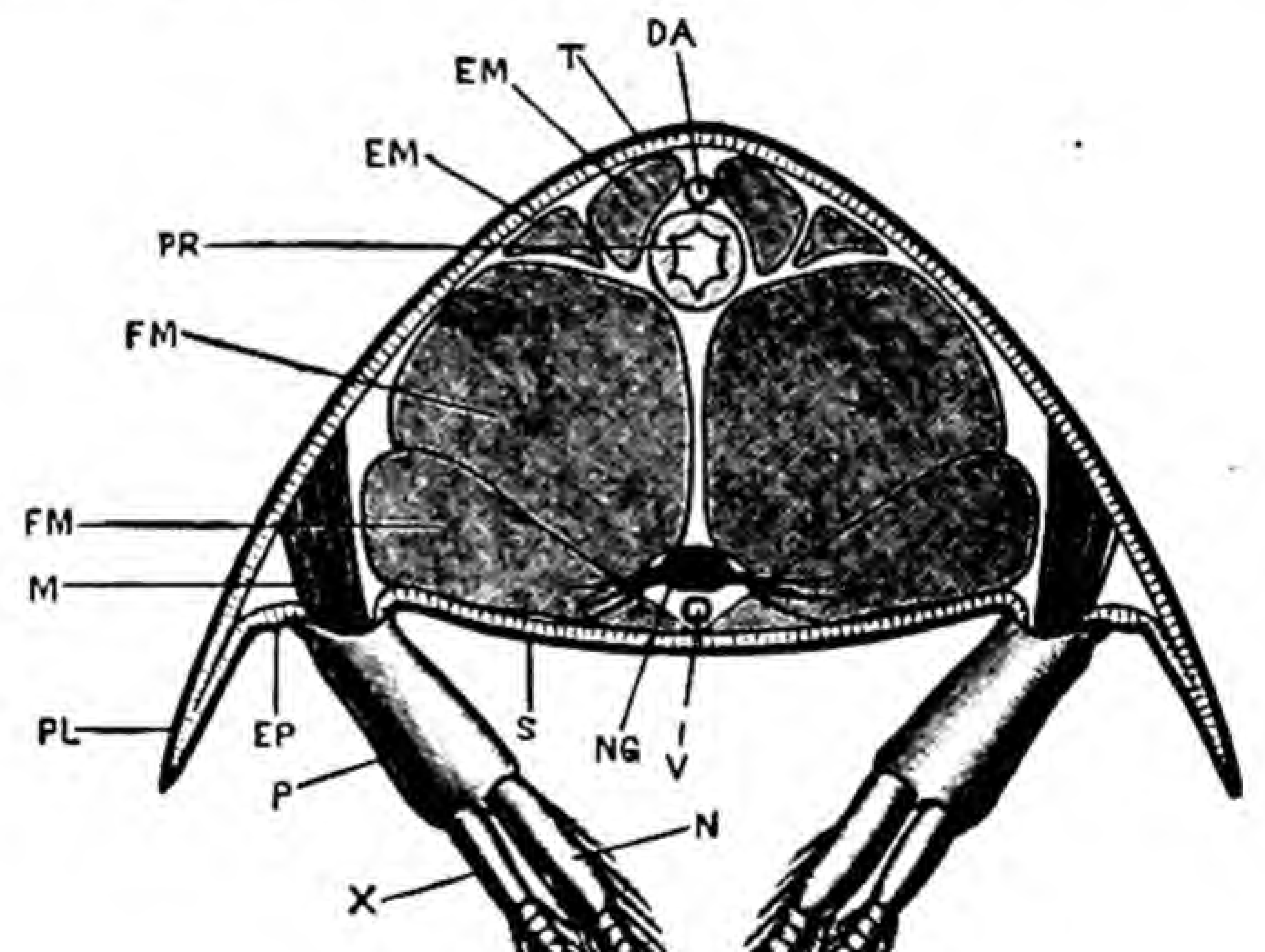


FIG. 365.—Transverse section of abdomen of **Crayfish.** DA, dorsal abdominal artery; EM, dorsal muscles of the abdomen; EP, space between the pleuron and the appendage; FM, ventral muscles of the abdomen; *M*, muscles of the appendage; N, endopodite; NG, nerve-ganglion; P, protopodite; PL, pleuron; PR, hind-gut; S, sternum; T, tergum; V, ventral abdominal artery; X, exopodite. (From Parker's *Practical Zoology*, after Marshall and Hurst.)

from the dorsal and lateral regions of both head and thorax, and is free only at the sides of the thorax, where it forms a flap or *gill-cover*, called branchiostegite (*bc.*), on each side, separated from the actual body-wall by a narrow space in

which the gills are contained (Fig. 372, *k.*). The carapace is made of chitin, strongly impregnated with carbonate of lime so as to be hard and but slightly elastic.

The **abdomen** is made up of six segments and a tail-piece or *telson*: the six segments (15–20) have a ring-like form, presenting a broad dorsal region or *tergum*, a narrow ventral region or *sternum*, and downwardly directed lateral processes, the *pleura*—the last quite unrepresented in Apus. The *telson* is flattened horizontally, and divided by a transverse groove into anterior and posterior portions. All the segments and the telson are calcified, and are united to one another by chitinous articular membranes: the first segment is similarly joined to the thorax. Thus the exo-skeleton of Astacus resembles that of Apus in being a continuous cuticular structure, but differs from it in being discontinuously calcified, so as to have the character of a hard jointed armour.

It has been stated that the abdominal segments are movable upon one another in a vertical plane—*i.e.* the whole abdomen can be *extended* or straightened, and *flexed* or bent under the cephalothorax: the segments are incapable of movement from side to side. This is due to the fact that, while adjacent segments are connected dorsally and ventrally by flexible articular membranes, they present at each side a *hinge* (Fig. 369, *h*), placed at the junction of the tergum and pleuron, and formed by a little peg-like process of one segment fitting into a depression or socket in the other. A line drawn between the right and left hinges constitutes the *axis of articulation*, and the only possible movement is in a plane at right angles to this axis.

Owing to the presence of the carapace, the **thoracic region** is immovable, and shows no distinction into segments either on its dorsal (tergal) or lateral (pleural) aspect. But on the ventral surface the sterna of the thoracic segments are clearly marked off by transverse grooves, and the hindmost of them is slightly movable. Altogether eight thoracic segments can be counted.

The ventral and lateral regions of the thoracic exoskeleton are produced into the interior of the body in the form of a segmental series of calcified plates, so arranged as to form a row of lateral chambers in which the muscles of the limbs lie, and a median tunnel-like passage or *sternal canal*, containing the thoracic portion of the nervous system. The entire *endophragmal system*, as it is called, constitutes a kind of internal skeleton: its anterior end is formed by a plate, the *cephalic apodeme*, having the same anatomical relations as the similarly named structure in Apus.

The **head** exhibits no segmentation: its sternal region is formed largely by a shield-shaped plate, the *epistoma*, nearly vertical in position. The ventral surface of the head is, in fact, bent so as to face forwards instead of downwards. The epistoma is bounded laterally by the free edge of the carapace instead of passing insensibly into it like the sub-frontal area of Apus, with

which, however, it agrees in having the *labrum* attached to the middle of its posterior border. The cephalic region of the carapace is produced in front into a large median spine, the *rostrum* (Fig. 364, *rs.*) : immediately below it is a plate from which spring two movably articulated cylindrical bodies, the *eye-stalks*, bearing the eyes at their ends.

The **appendages** are seen at a glance to differ from those of Apus in their vastly greater degree of differentiation : obvious at a glance are the long feelers

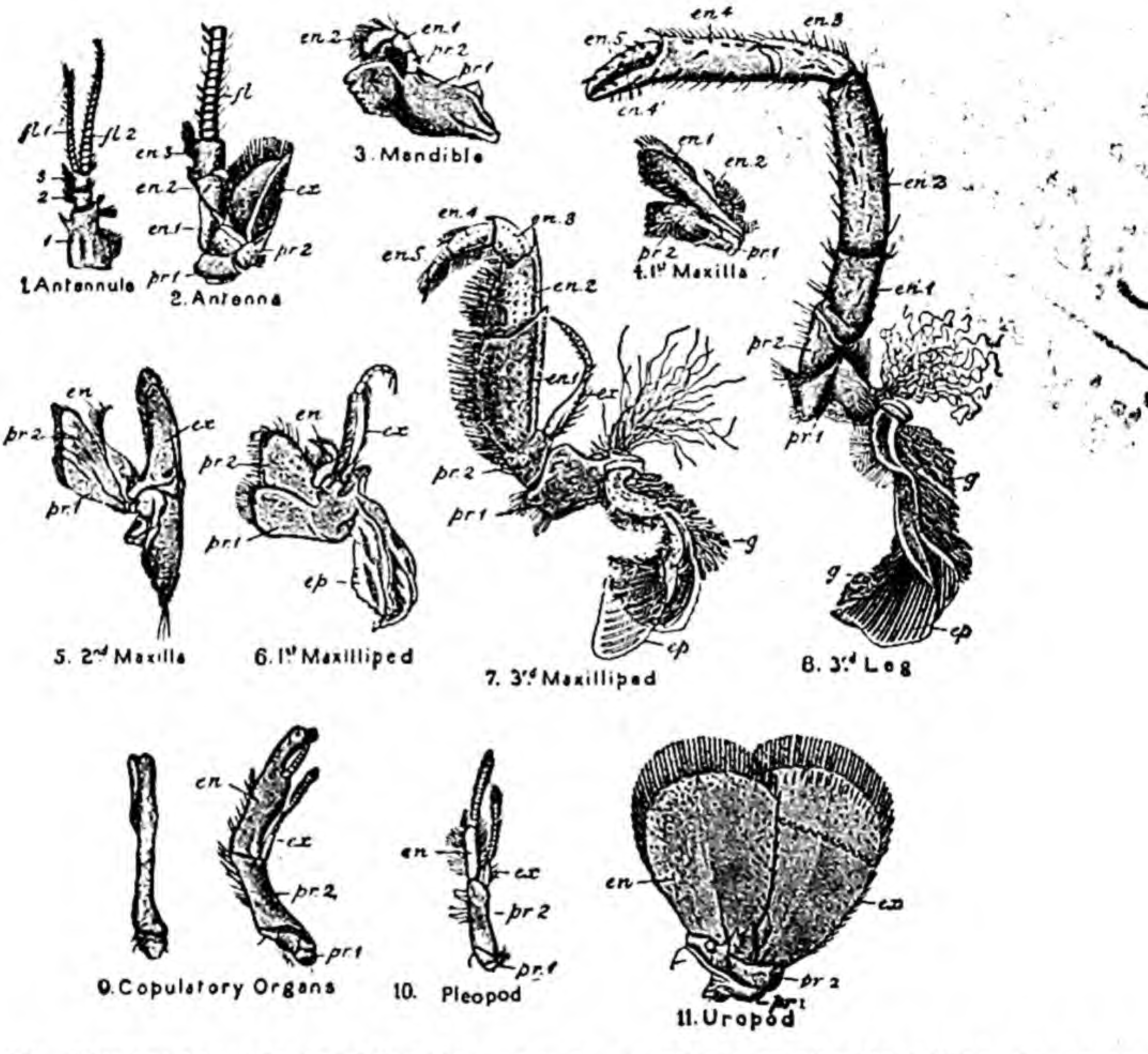


FIG. 366.—Typical appendages of **Astacus.** *en. 1—5*, podomeres of endopodite ; *ep.*, epipodite ; *ex.* exopodite ; *fl.* flagella ; *g.* gill ; *pr. 1, pr. 2*, podomeres of protopodite ; *1—3*, podomeres of axis of antennule. (After Huxley.)

(Fig. 364, *an′*, *an″*.) attached to the head, the five pairs of legs springing from the thorax, and the little fin-like bodies arising from the sterna of the abdomen. It will be convenient to begin with the last-named region.

The third, fourth, and fifth segments of the abdomen bear each a pair of small appendages, the swimmerets or *pleopods* (Fig. 366, *10*), the resemblance of which to the biramous limbs of the larval Apus is obvious. There is an axis or *protopodite* consisting of a very short proximal (*pr. 1*) and a long distal

(*pr. 2*) podomere, and bearing at its free end two jointed plates, fringed with setæ, the *endopodite* (*en.*) and *exopodite* (*ex.*). These appendages act as fins, moving backwards and forwards with a regular swing, and probably aiding in the animal's forward movements.

In the female a similar appendage is borne on the second segment, while that of the first is more or less vestigial. In the male the first and second pleopods (*9*) are modified into incomplete tubes which act as copulatory organs, serving to transfer the spermatophores to the body of the female. The sixth pair of abdominal limbs (*11*) are alike in the two sexes: they are very large, both endopodite and exopodite having the form of broad flat plates: in the natural position of the parts they lie one on each side of the telson, forming with it a large five-lobed tail-fin capable of being spread out after the manner of a fan; they are therefore conveniently called *uropods* or tail-feet. The telson itself bears no appendages.

The thoracic appendages are very different. The four posterior segments bear long, slender, jointed *legs* (*8*), upon which the animal walks: in front of these is a pair of very large legs terminating in huge claws or *chelæ* (Fig. 364, *ch.*), and hence called *chelipeds*. The three anterior segments bear much smaller appendages more or less leg-like in form, but having their bases toothed to serve as jaws: they are distinguished as *maxillipeds* or foot-jaws (Fig. 366, *6*, *7*).

The structure of these appendages is best understood by a consideration of the *third maxilliped* (*7*). The main portion of the limb is formed of seven podomeres arranged in a single series, strongly calcified, and—with the exception of the second and third, which are fused—movably articulated with one another. The second podomere, counting from the proximal end, bears a many-jointed feeler-like organ (*ex.*), and from the first springs a thin folded plate (*ep.*) having a plume-like gill (*g.*) attached to it. Obviously such an appendage is biramous, but with one of its branches greatly in excess of the other: the first two segments of the axis (*pr. 1*, *pr. 2*) form the protopodite, its remaining five segments (*en. 1–5*) the endopodite, and the feeler, which is directed outwards, or away from the median plane, the exopodite (*ex.*). The folded plate (*ep.*) is called the *epipodite*: in the natural position of the parts it is directed upwards, and lies in the gill-cavity between the proper wall of the thorax and the gill-cover (Fig. 372).

The five *legs* (*8*) differ from the third maxilliped in their greater size, and in having no exopodite: in the fifth or last the epipodite also is absent. The first three of them have undergone a curious modification, by which their ends are converted into pincers or *chelæ*: the fourth segment (*en. 4*) of the endopodite (sixth of the entire limb) is produced distally so as to form a claw-like projection (*en.* 4^1), against which the terminal segment (*en. 5*) bites. The first leg is much stouter than any of the others, and its chela is of immense size and forms an

important weapon of offence and defence. The *second maxilliped* resembles the third, but is considerably smaller: the *first* (*6*) has its endopodite greatly reduced, the two segments of its protopodite large and leaf-like, and no gill is connected with the epipodite.

As in Apus, the head bears a pair of mandibles and two pairs of maxillæ in relation with the mouth, and in front of that aperture a pair of antennules and one of antennæ. The hindmost appendage of the head is the *second maxilla* (*5*), a markedly foliaceous appendage: its protopodite (*pr. 1*, *pr. 2*) is cut up into lobes comparable with the four proximal endites in the thoracic feet of Apus: its endopodite (*en.*) corresponds with the fifth endite, while the sixth endite is represented by the exopodite (*ex.*), modified into a boomerang-shaped plate, which, as we shall see, is an important accessory organ of respiration. The *first maxilla* (*4*) is a very small organ, having neither exopodite nor epipodite. The *mandible* (*3*) is a large strongly calcified body, toothed along its inner edge, and bearing on its anterior border a little three-jointed feeler-like body, the *palp*, the two distal segments (*en. 1*, *en. 2*) of which represent the endopodite, its proximal segment (*pr. 2*) together with the mandible proper (*pr. 1*), the protopodite.

The *antenna* (*2*) is of great size, being nearly as long as the whole body. It consists of an axis of five podomeres, the fifth or last of which bears a long, flexible, many-jointed structure, or *flagellum* (*fl.*) while from the second segment springs a scale-like body or *squame* (*ex.*). It is fairly obvious that the two proximal segments represent the protopodite, the remaining three, with the flagellum, the endopodite, and the squame the exopodite.

The *antennule* (*1*) has an axis of three podomeres (*1–3*) ending in two many-jointed flagella (*fl. 1*, and *2*). There is no exact correspondence between the parts of the antennule and those of the remaining appendages.

The *eye-stalks*, already noticed, arise just above the antennules and are formed each of a small proximal and a large distal segment. They were sometimes counted as appendages serially homologous with the antennæ, legs, etc. But, as we have seen in the case of Apus, the appendages of Crustacea are always formed in regular order from before backwards; the eye-stalks, on the other hand, always appear later, both in individual development and in the Crustacean series, than the normal anterior appendages. They are therefore to be looked upon as articulated processes developed in connection with the need for an increased range of vision.

The body of the Crayfish consists of a pre-segmental region, corresponding to the prostomium of the Annelids, followed by twenty metameres of which the first, the so-called pre-antennulary metamere, is purely embryonic and is not represented by any appendages. The telson is not a metamere but is to be looked upon as a post-segmental region. The eye-stalks belong to the pre-segmental region, which together with the first metameres forms the head.

The antennules, antennæ, mandibles, first and second maxillæ, belonging to metameres *2–6*, are to be regarded as head appendages. The next eight metameres (*7–14*) constitute the thorax and bear the three pairs of maxillipeds, the chelipeds, and the four pairs of walking legs. The remaining six metameres (*15–20*) together with the telson constitute the abdomen and bear five pairs of pleopods (four in the female) and one pair of uropods.

The **articulation** of the various podomeres of the appendages is on the same plan as that of the abdominal segments (p. 399). The podomeres are, it must be remembered, rigid tubes: they are connected with one another by flexible *articular membranes* (Fig. 367, *art. m.*), but at two points the adjacent ends of the tubes come into contact with one another and are articulated by peg-and-socket joints (*h.*), the two joints being at opposite ends of a diameter which forms the *axis of articulation.* The two podomeres can, therefore, be moved upon one another in a plane at right angles to the axis of articulation and in no other direction, the joints being pure hinge-joints. As a rule, the range of movement is from the perpendicular to a tolerably extensive flexion on one side—the articulations are single-jointed, like our own elbows and knees. The whole limb is, however, capable of universal movement, owing to the fact that the axes of articulation vary in direction in successive joints: the first joint of a limb bending, for instance, up and down, the next backwards and forwards, the next obliquely, and so on. In some cases, *e.g.* in the pleopods, peg-and-socket joints are absent, the articulation being formed merely by an annular articular membrane, and movement being therefore possible in any plane.

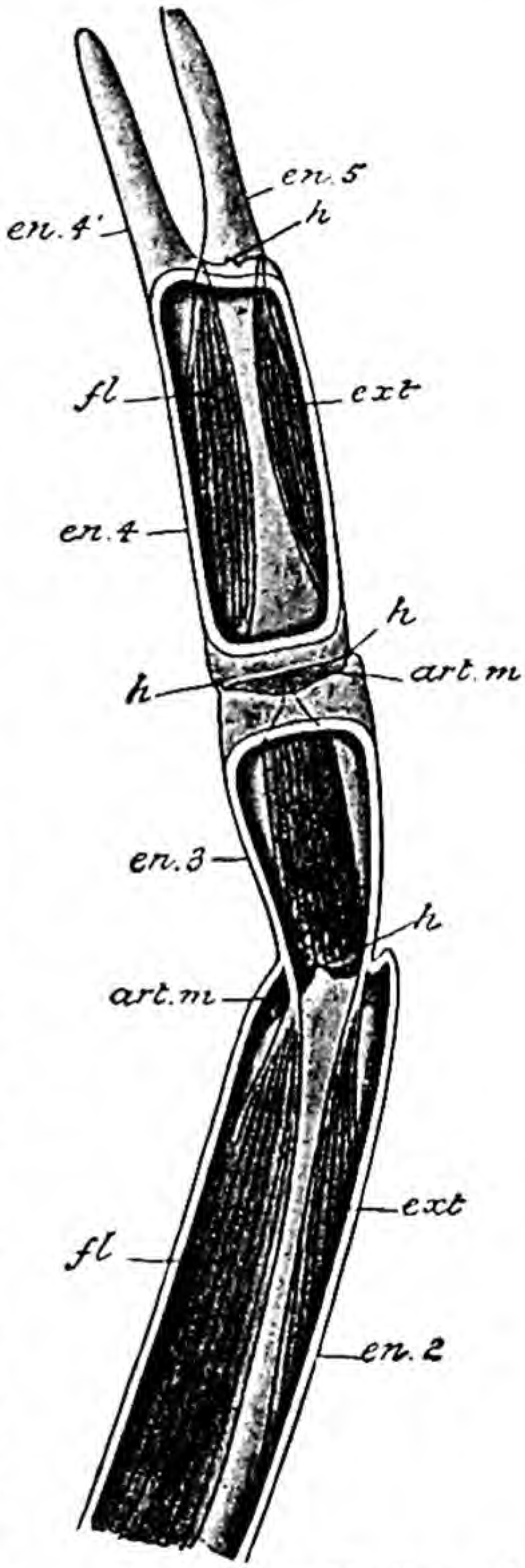


FIG. 367.—Portion of a leg of **Astacus**, with the exoskeleton partly removed, showing articulations and muscles. *art. m.* articular membrane; *en.* 2—5, podomeres of endopodite; *ext.* extensor muscles; *fl.* flexors; *h.* hinge.

Body-wall.—The exoskeleton is produced into spines of varying form and size, and many parts of it bear tufts or fringes of setæ, which also exhibit a wide variation in size and form. It is composed of a thick laminated chitinous membrane (Fig. 368, *cu.*), more or less impregnated with lime-salts, and is shed periodically—once a year during adult life. Beneath it is the epidermis (*ep.*) composed of a single layer of cells from

which the chitin is secreted, and underlain by a layer of connective-tissue (*c.t.*) to which the muscles are attached.

The **muscular system,** like the exoskeleton, shows a great advance in complexity over that of Apus. In the abdomen (Fig. 369) the muscles are of great size, and are divisible into a smaller dorsal and a larger ventral set. The *dorsal muscles* (*d. m.*) are paired longitudinal bands, divided into myomeres, and inserted by connective-tissue into the anterior border of each segment: anteriorly they are traceable into the thorax, where they arise from the side-walls of that region. When these muscles contract, they draw the anterior edge of each tergum under the posterior edge of its predecessor, and thus extend or straighten the abdomen.

The *ventral muscles* are extraordinarily complex. Omitting details, there is on each side a wavy longitudinal band of muscle (*c. m.*), nearly circular in section, which sends off a slip (*ex.*) to be inserted into each segment above the hinge (*h.*): the contraction of this muscle must obviously tend to approximate the terga, and so aid the dorsal muscles in extending the abdomen. Around this *central muscle* is wrapped, in each segment, a band of muscle (*env. m.*) in the form of a loop, the outer limb of which turns forwards and is inserted into a sternum, while the inner limb turns backwards and is inserted into another and more posterior sternum. The contraction of this *enveloping muscle* produces an

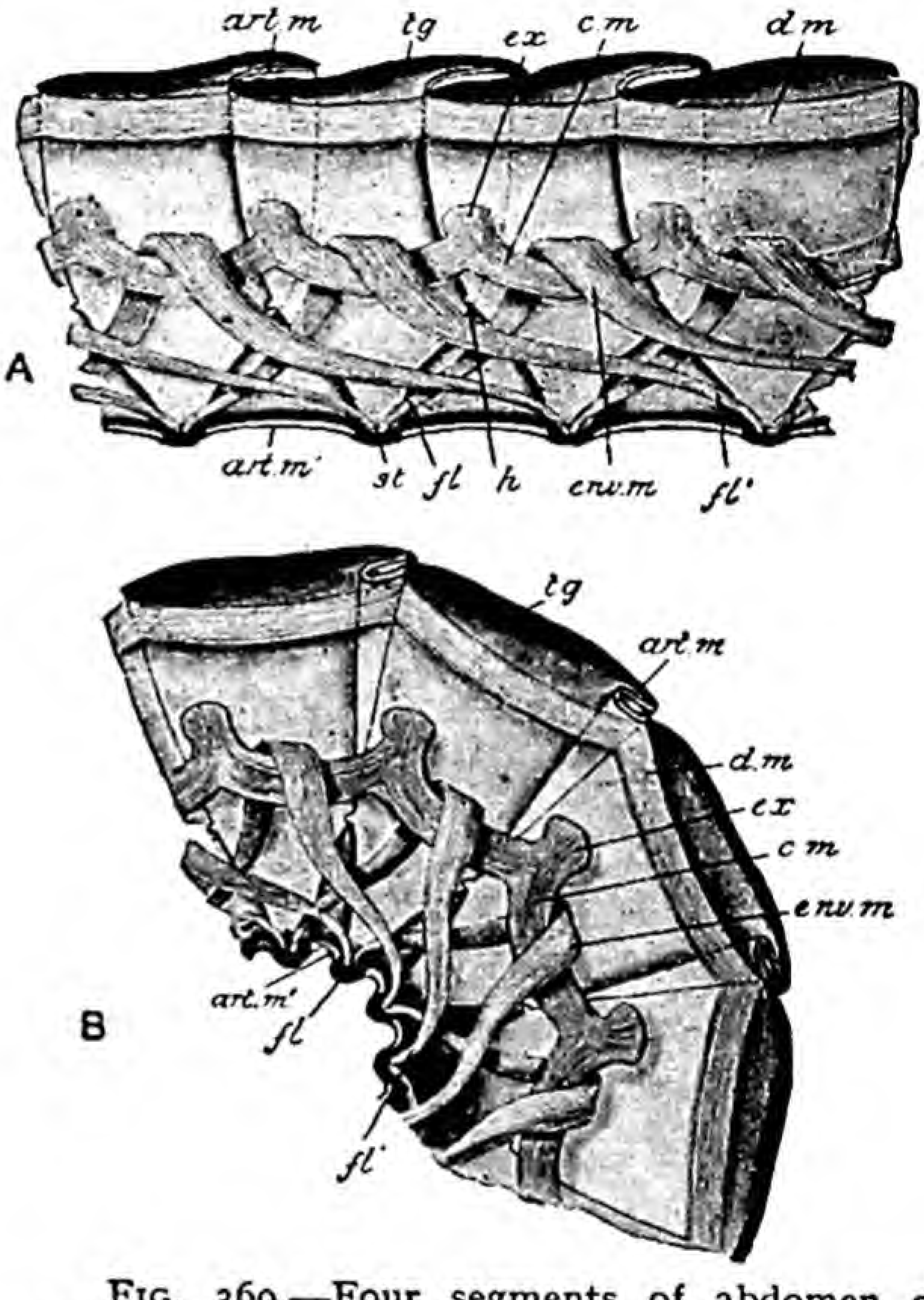


FIG. 369.—Four segments of abdomen of **Crayfish** in sagittal section with muscles (diagrammatic). *A*, extension; *B*, flexion; *art. m.*, *art. m'.* articular membranes; *c. m.* central muscles; *d. m.* dorsal muscle; *ex.* extensor slip of central muscle; *env. m.* enveloping muscle; *fl.*, *fl.*[1], flexor slips; *h.* hinge; *st.* sternum; *tg.* tergum.

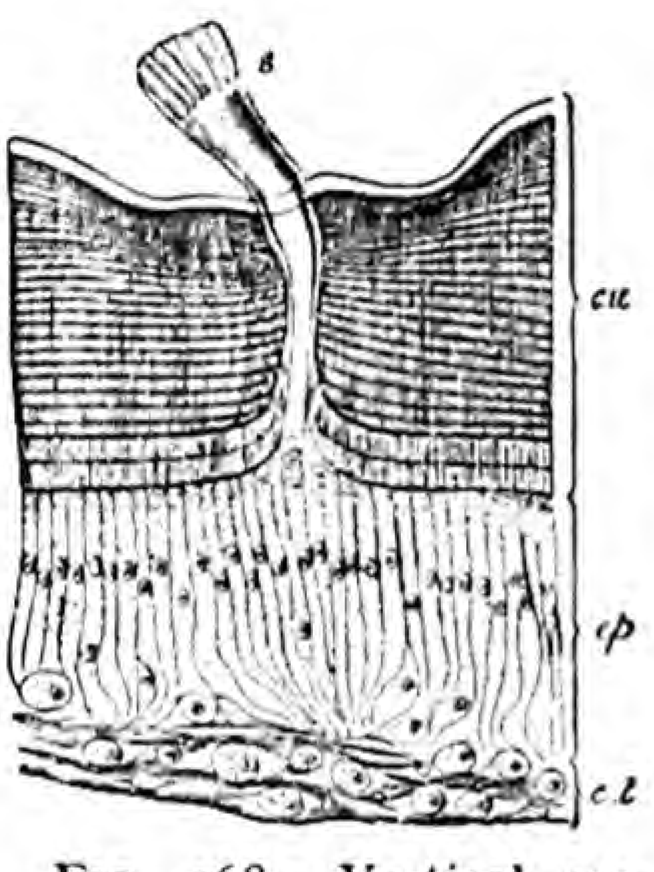


FIG. 368.—Vertical section of skin and exoskeleton of **Lobster.** *c. t.* connective-tissue; *cu.* cuticle; *ep.* epidermis; *s.* seta. (After Gerstaecker.)

approximation of the sterna, and thus flexes the abdomen, the central muscle always keeping the middle of the loop in place. The ventral muscles are, like the dorsal, traceable into the thorax, where they arise from the endophragmal system (p. 399): their various parts are connected by a complex system of fibres extending between the central and enveloping muscles, and connecting both with their fellows of the opposite side. The flexor muscles are immensely powerful, and produce, when acting together, a sudden and violent bending of the abdomen upon the cephalothorax, causing the Crayfish to dart backwards with great rapidity.

It will be seen that the body-muscles of the Crayfish cannot be said to form a layer of the body-wall, as in Chætopods, the abdomen of Apus, etc., but constitute an immense fleshy mass, filling up the greater part of the body-cavity, and leaving a very small space around the enteric canal.

In the limbs (Fig. 367) each podomere is acted upon by two muscles situated in the next proximal podomere. These muscles are inserted, by chitinous and often calcified tendons, into the proximal edge of the segment to be moved, the smaller on the extensor (*ext.*), the larger on the flexor (*fl.*) side, in each case half-way between the two hinges, so that a line joining the two muscular insertions is at right angles to the axis of articulation.

The **digestive organs** are constructed on the same general plan as those of Apus, but present many striking differences (Fig. 370). The *mouth* (*m.*), lies in the middle ventral line of the head, and is bounded in front by the labrum, at the sides by the mandibles, and behind by a pair of delicate lobes, the *paragnatha*. It leads by a short wide *gullet* (*œ.*) into a capacious *stomach* which occupies a great part of the interior of the head, and is divided into a large anterior division, the *cardiac chamber* (*st.*), and a small posterior division, the *pyloric chamber* (*py.*): the latter passes into a narrow and very short portion of the intestine, the *mid-gut* (*m.g.*), from which the rest of the intestine (*int.*) extends to the *anus* (*a.*), situated on the ventral surface of the telson.

The outer layer of the enteric canal consists of connective-tissue containing striped muscular fibres: within this is a single layer of columnar epithelial cells. In the gullet and stomach, and in the hind-gut, the epithelium secretes a layer of chitin, which thus constitutes the innermost lining of those cavities. It is proved by development that the mid-gut, which has no chitinous lining, is the only part of the enteric canal developed from the mesenteron: the gullet and stomach arise from the stomodæum, the hind-gut from the proctodæum. Thus a very small portion of the enteric epithelium is endodermal.

In the cardiac chamber the chitinous lining is thickened and calcified in certain parts, so as to form a complex articulated framework, the "*gastric mill*," on which are borne a median and two lateral *teeth*, strongly calcified and projecting into the cavity. Two pairs of strong muscles arise from the carapace, and are inserted into the cardiac chamber: when they contract they move the

mill in such a way that the three teeth meet in the middle and complete the comminution of the food begun by the jaws. The separation of the teeth is effected partly by the elasticity of the mill, partly by delicate muscles in the walls of the stomach. The pyloric division of the stomach forms a strainer: its walls are thickened and produced into numerous setæ, which extend quite across the narrow lumen and prevent the passage of any but finely divided particles into the intestine. Thus the stomach has no digestive function, but is merely a masticating and straining apparatus. On each side of the anterior

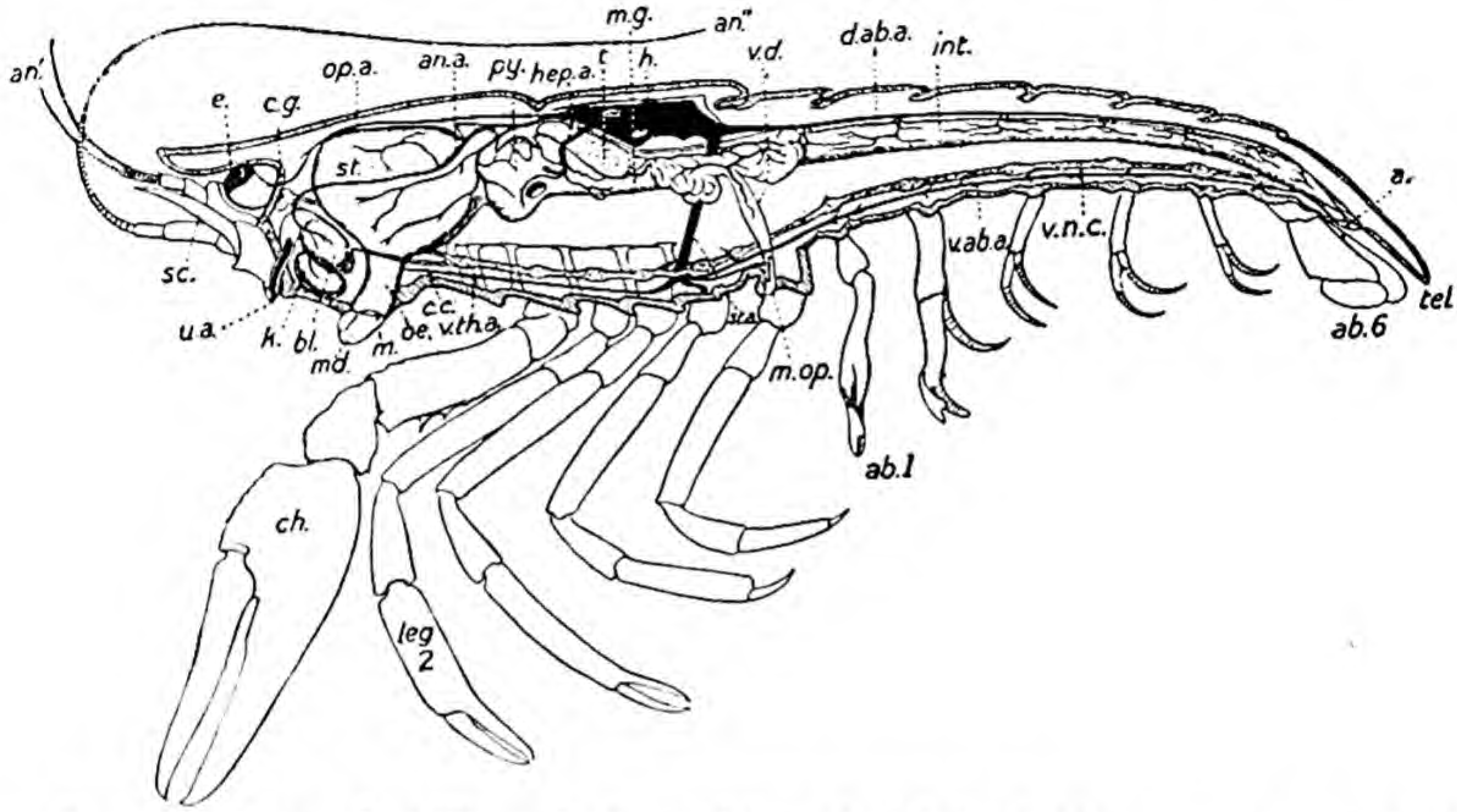


FIG. 370.—**Astacus fluviatilis**, male dissected from the left hand side. *a.* anus; *ab. 1*, first abdominal appendage (pleopod); *ab. 6*, last abdominal appendage (uropod); *an'.* antennule; *an''.* antenna; *an. a.* antennary artery; *bl.* bladder; *c.c.* circum-œsophageal connective; *c. g.* cerebral ganglion; *ch.* chela; *d. ab. a.* dorsal abdominal artery; *e.* eye; *h.* heart; *hep. a.* hepatic artery; *int.* intestine; *k.* kidney (green gland); *leg. 2*, first walking leg; *m.* mouth; *md.* mandible; *m. g.* mid-gut; *m. op.* male genital opening; *œ.* œsophagus; *op. a.* ophthalmic artery; *py.* pyloric chamber; *sc.* scale of antenna; *st.* cardiac chamber of stomach; *st. a.* sternal artery; *t.* testis; *tel.* telson; *u. a.* urinary aperture; *v. ab. a.* ventral abdominal artery; *v. d.* vas deferens; *v. n. c.* ventral nerve-cord; *v. th. a.* ventral thoracic artery. (From Shipley and MacBride's *Zoology* (University Press Cambridge).)

division is found at certain seasons of the year a plano-convex mass of calcareous matter, the *gastrolith*.

The digestion of the food and to some extent the absorption of the digested products are performed by a pair of large glands, lying one on each side of the stomach and anterior end of the intestine. They are formed of finger-like sacs or *cæca*, which discharge into wide ducts opening into the mid-gut, and are lined with glandular epithelium derived from the endoderm of the embryo. The glands are often called livers, but as the yellow fluid they secrete digests protein as well as fat, the name *hepato-pancreas* is often applied to them, or they may be

called simply *digestive glands*. The Crayfish is carnivorous, its food consisting largely of decaying animal matter. Microscopic glands occur in the wall of the gullet.

The digestive organs and other viscera are surrounded by a *body-cavity*, which is in free communication with the blood-vessels and itself contains blood. As will be pointed out more particularly hereafter, this cavity is to be looked upon as an immense blood-sinus, and not as a true cœlome.

There are well-developed **respiratory organs,** in the form of *gills*, contained in a narrow branchial chamber, bounded internally by the proper wall of the thorax (Fig. 372, *ep*.), externally by the gill-cover (*branchiostegite*) or pleural region of the carapace (*kd*.). Each gill consists of a stem giving off numerous branchial filaments, so that the whole organ is plume-like. The filaments are hollow, and communicate with two parallel canals in the stem—an external, the *afferent branchial vein*, and an internal, the *efferent branchial vein*. The gill is to be considered as an out-pushing of the body-wall, and contains the same layers—a thin layer of chitin externally, then a single layer of epithelial cells, and beneath this connective-tissue, hollowed out for the blood channels and containing gland-cells, which will be referred to presently.

According to their point of origin, the gills are divisible into three sets—first, *podobranchiæ* or foot-gills, springing from the epipodites of the thoracic appendages, from which they are only partially separable; secondly, *arthrobranchiæ* or joint-gills, springing from the articular membranes connecting the thoracic appendages with the trunk; and thirdly, *pleurobranchiæ*, or wall-gills, springing from the lateral walls of the thorax, above the attachment of the appendages. It is inferred from the study of other Crayfishes, that a typical thoracic segment bears four gills, one podobranch, two arthrobranchs, and one pleurobranch. But in Astacus one or more of the gills in every segment are absent or vestigial, and the table, or "branchial formula," shows the actual number and arrangement of these organs, *ep* standing for epipodite, and *r* for the vestige of a gill.

By adding up the columns vertically we get the number of gills in each segment; by adding them horizontally, the number of each kind of gill; and by adding together the results obtained by both methods, the total number of gills, viz., eighteen complete gills with two vestiges and seven epipodites.

Thoracic Segments.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	Total.
Podobranchiæ .	0+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	0	6+7*ep*
Arthrobranchiæ	0	1	2	2	2	2	2	0	11
Pleurobranchiæ	0	0	0	0	0	*r*	*r*	1	1+2*r*
Total	0+*ep*	2+*ep*	3+*ep*	3+*ep*	3+*ep*	3+*r*+*ep*	3+*r*+*ep*	1	18+2*r*+7*ep*

The **excretory organs** differ both in position and in form from those of Apus. There are no shell-glands, but at the base of each antenna is an organ of a greenish colour, the *antennary* or *green gland*, by which the function of renal excretion is performed. The gland (Fig. 371) is cushion-shaped, and consists of three parts—(1) a central *saccule* (*s.*) of a yellowish colour, occupying the mid-dorsal region, and consisting of a sac divided into numerous compartments by

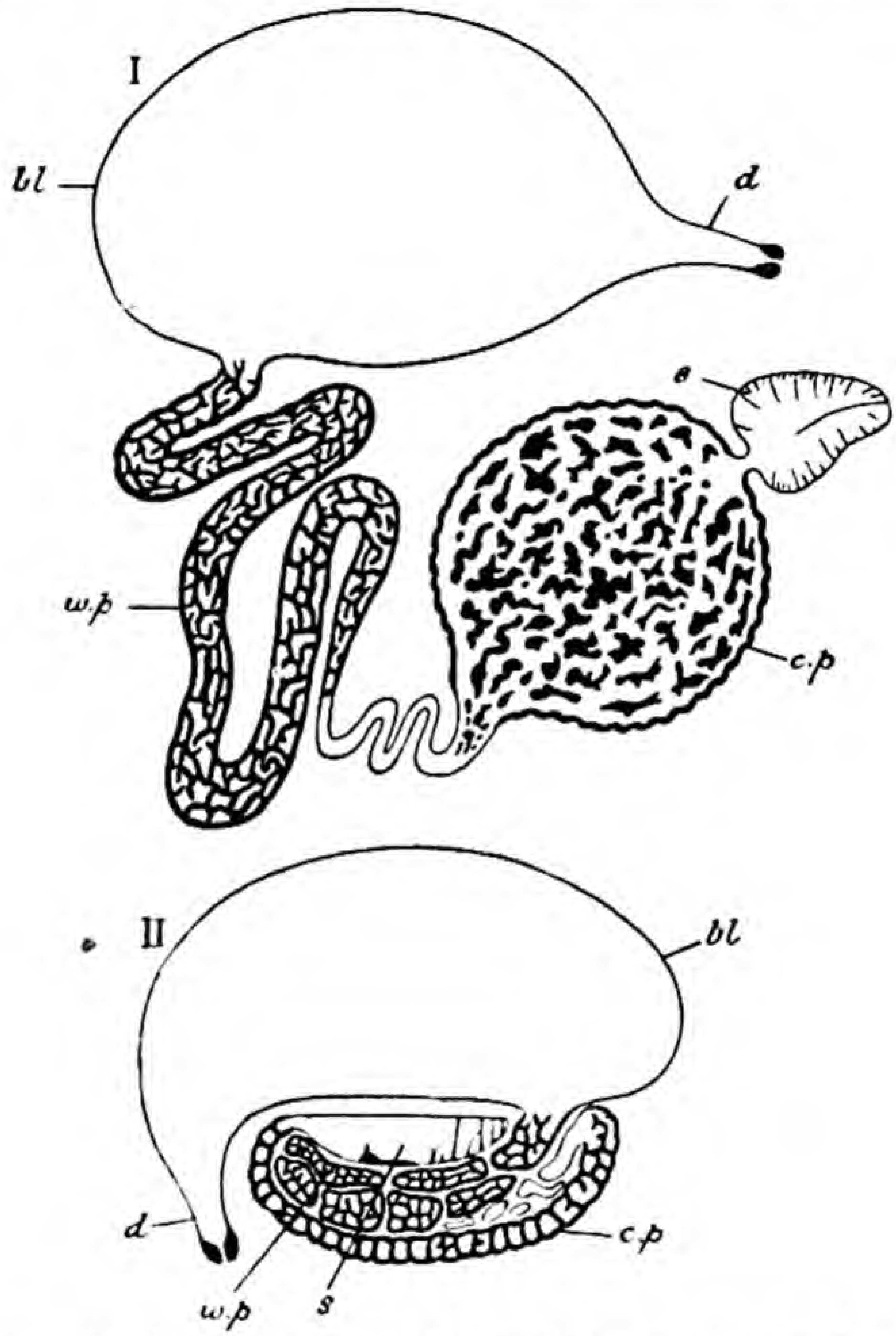


FIG. 371.—Diagram of kidney of **Astacus fluviatilis.** I, unravelled; II, the parts in their natural relations. *bl.* bladder; *c. p.* cortical portion; *d.* duct; *s.* saccule; *w. p.* white portion. (After Marchal.)

partitions, and communicating with (2) the outer or *cortical portion* (*c. p.*), of a green colour, consisting of a glandular network formed of anastomosing canals, and communicating in its turn with (3) a *white portion* (*w. p.*), formed of a single tube partly converted into a sponge-work by ingrowths of its walls. The whole organ is lined by glandular epithelium, and the white portion discharges into a thin-walled sac or *urinary bladder* (*bl.*) which opens by a *duct* (*d.*) on the proximal segment of the antenna. The glands already referred to as occurring in the gills are also supposed to have an excretory function.

The **circulatory organs** are in a high state of development. The *heart* (Figs. 370, 372, *h.*) is situated in the dorsal region of the thorax, and is a roughly polygonal muscular organ pierced by three pairs of apertures or *ostia*, guarded by valves which open inwards. It is enclosed in a spacious *pericardial sinus* (Fig. 372, *pc.*), which contains blood. From the heart spring a number of narrow tubes, called *arteries*, which serve to convey the blood to various parts of the body. At the origin of each artery from the heart are valves which allow of the flow of blood in one direction only, viz., from the heart to the artery. From the anterior end of the heart arise five vessels—the median *ophthalmic artery* (Fig. 370, *op. a.*), which passes forwards to the eyes; paired *antennary arteries* (*an. a.*), going to the antennules, antennæ, green glands, etc., and sending off branches to the stomach; and paired *hepatic arteries* (*hep. a.*), going to the digestive glands. The posterior end of the heart gives off two unpaired arteries practically united at their origin, the *dorsal abdominal artery* (*d. ab. a.*), which passes backwards above the intestine, sending branches to it and to the dorsal muscles; and the large *sternal artery* (*st. a.*), which extends directly downwards, indifferently to right or left of the intestine, passing between the connectives uniting the third and fourth thoracic ganglia, and then turns forwards and runs in the sternal canal, immediately beneath the nerve-cord, sending off branches to the legs, jaws, etc. At the point where the sternal artery turns forwards it gives off the median *ventral abdominal artery* (*v. ab. a.*), which passes backwards beneath the nerve-cord, and supplies the ventral muscles, pleopods, etc.

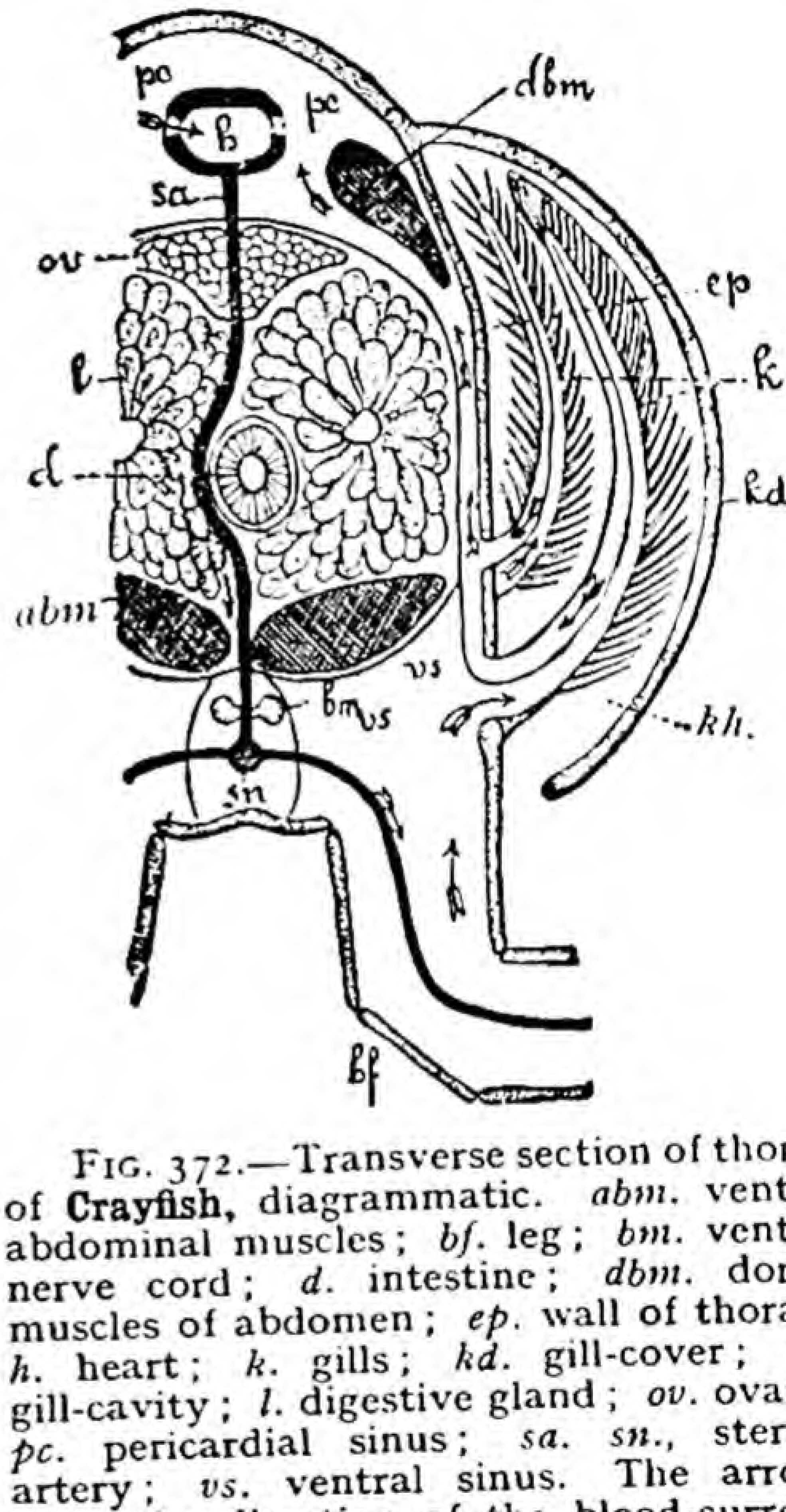


FIG. 372.—Transverse section of thorax of **Crayfish,** diagrammatic. *abm.* ventral abdominal muscles; *bf.* leg; *bm.* ventral nerve cord; *d.* intestine; *dbm.* dorsal muscles of abdomen; *ep.* wall of thorax; *h.* heart; *k.* gills; *kd.* gill-cover; *kh.* gill-cavity; *l.* digestive gland; *ov.* ovary; *pc.* pericardial sinus; *sa. sn.*, sternal artery; *vs.* ventral sinus. The arrows show the direction of the blood-current. (From Lang's *Comparative Anatomy.*)

All these arteries branch extensively in the various organs they supply, becoming divided into smaller and smaller offshoots, which finally end in microscopic vessels called *capillaries*. These latter end by open mouths which communicate with the *blood-sinuses* (Fig. 373, *s.*), spacious cavities lying among the muscles and viscera, and all communicating, mediately or immediately, with the *sternal sinus* (*st.s.*), a great median canal running longitudinally along

the thorax and abdomen, and containing the ventral nerve-cord and the sternal and ventral abdominal arteries. In the thorax the sternal sinus sends an offshoot to each gill in the form of a well-defined vessel, which passes up the outer side of the gill and is called the *afferent branchial vein* (*af.br.v.*; see also Fig. 372). Spaces in the gill-filaments place the *afferent* in communication with the *efferent branchial vein* (*ef.br.v.*), which occupies the inner side of the gill-stem. The eighteen efferent branchial veins open into six *branchiocardiac veins* (*br.c.v.*), which pass dorsally in close contact with the lateral wall of the thorax and open into the pericardial sinus (*pcd.s.*).

The whole of this system of cavities is full of blood, and the heart is rhythmically contractile. When it contracts, the blood contained in it is prevented from entering the pericardial sinus by the closure of the valves of the ostia, and therefore takes the only other course open to it, viz., into the arteries.

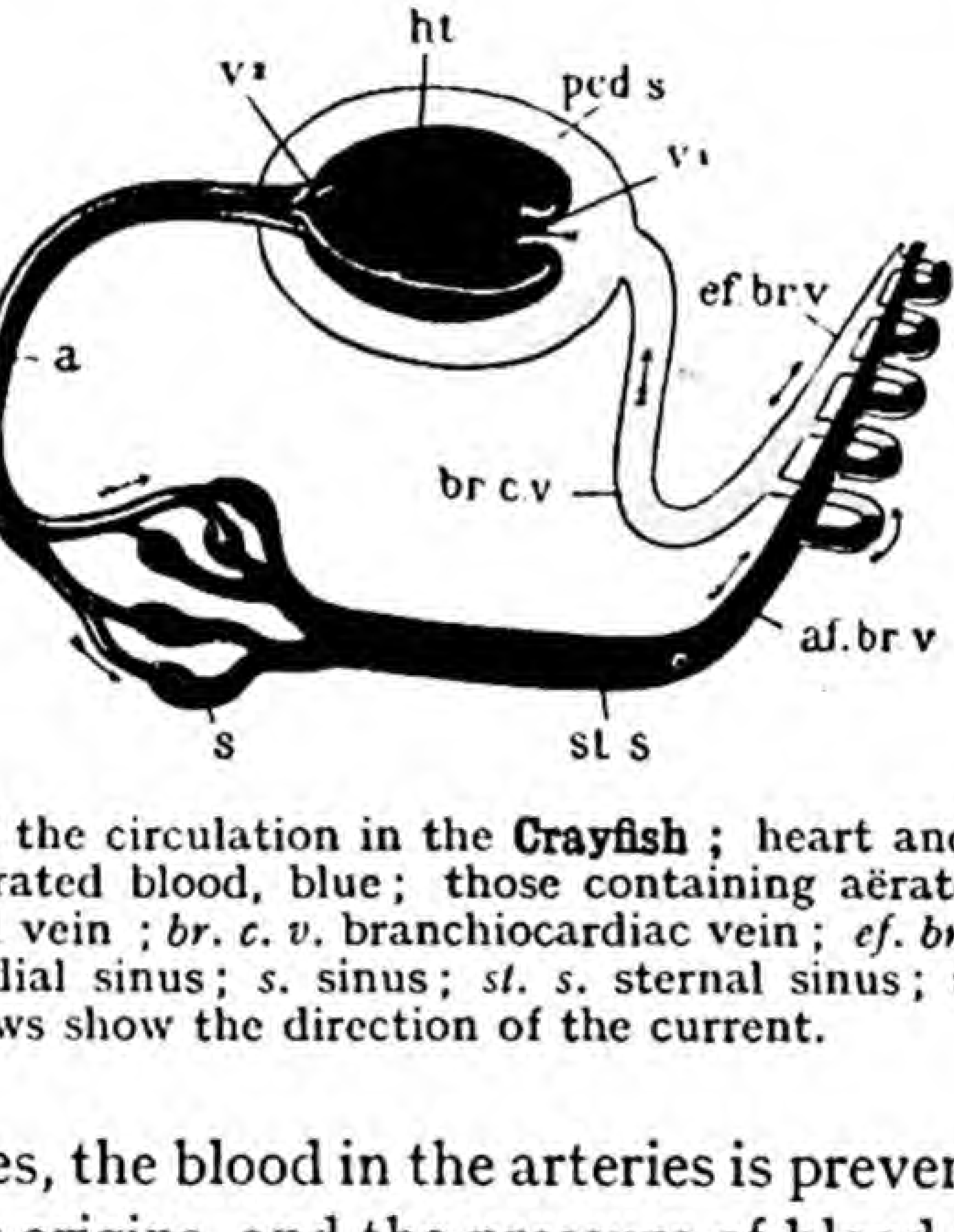


FIG. 373.—Diagram of the circulation in the **Crayfish**; heart and arteries scarlet, veins and sinuses containing non-aërated blood, blue; those containing aërated blood, pink. *a.* artery; *af. br. v.* afferent branchial vein; *br. c. v.* branchiocardiac vein; *ef. br. v.* efferent branchial vein; *ht.* heart; *pcd. s.* pericardial sinus; *s.* sinus; *st. s.* sternal sinus; v^1. ostium with valves; v^2. arterial valves. The arrows show the direction of the current.

When the heart relaxes, the blood in the arteries is prevented from regurgitating by the valves at their origins, and the pressure of blood in the pericardial sinus forces open the valves of the ostia and so fills the heart. Thus in virtue of the successive contractions of the heart and of the disposition of the valves, the blood is kept constantly moving in one direction—viz., from the heart by the arteries to the various organs of the body, where it receives carbon dioxide and other waste matters; thence by sinuses into the great sternal sinus; from the sternal sinus by afferent branchial veins to the gills, where it exchanges carbon dioxide for oxygen; from the gills by efferent branchial veins to the branchiocardiac veins, thence into the pericardial sinus, and so to the heart once more.

It will be seen that the circulatory system of the Crayfish consists of three sections—(1) the *heart* or organ of propulsion; (2) a system of outgoing channels,

the *arteries*, which carry the blood from the heart to the body generally; and (3) a system of returning channels, some of them, the *sinuses*, mere irregular cavities; others, the *veins*, with definite walls, which return it from the various organs back to the heart. The respiratory organs, it should be observed, are interposed in the returning current, so that blood is taken both to and from the gills by veins.

The blood when first drawn is colourless, but after exposure to the air takes on a bluish-grey tint. This is owing to the presence of a pigment called *hæmocyanin*, which becomes blue when combined with oxygen; it is a respiratory pigment, and serves, like hæmoglobin, as a carrier of oxygen from the external medium to the tissues. The hæmocyanin is contained in the plasma of the blood: the corpuscles are all colourless leucocytes.

The **nervous system** (Fig. 374) consists, like that of Apus, of a brain (*c.g.*) and a ventral nerve-cord, united by circum-œsophageal connectives (*c.c.*). But the right and left halves of the ventral cord have undergone partial fusion, so that the ganglia, and in the abdomen the connectives also, appear single instead of double. Moreover, the brain supplies not only the eyes and antennules, but the antennæ as well, and it is found by development that the two pairs of ganglia belonging to the antennulary and antennary segments have fused with the brain proper. Hence we have to distinguish between a primary brain or *archi-cerebrum*, the ganglion of the pre-segmental region, and a secondary brain, formed by the union with the archi-cerebrum of three pairs of ganglia, viz., the ganglia of the embryonic first metamere (*protocerebrum*), the ganglia of the second metamere (*mesocerebrum*) innervating the antennules, and the ganglia of the third metamere (*metacerebrum*) innervating the antennæ. A further case of concrescence of ganglia is seen in the ventral nerve-cord, where the ganglia of the last three cephalic and first three thoracic segments have united to form a large compound *sub-œsophageal ganglion* (*s.g.*). All the remaining segments have their own ganglia, with the exception of the telson, which is supplied from the ganglion of the preceding segment. There is a *viscera system* of nerves (*s.*) supplying the stomach, originating in part from the brain and in part from the circum-œsophageal connectives.

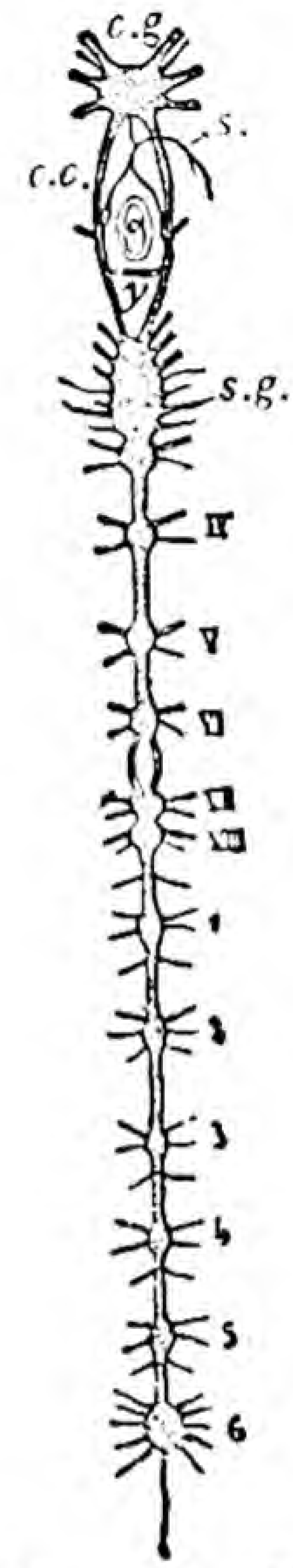


FIG. 374.—Nervous system of **Astacus fluviatilis.** *c. c.* circum-œsophageal connective; *c. g.* cerebral ganglion (brain); *s.* visceral nerve; *s. g.* sub-œsophageal ganglion; *y.* post-œsophageal commissure; IV—VIII, thoracic ganglia; *1*—*6*, abdominal ganglia. (From Lang's *Comparative Anatomy*, after Vogt and Yung.)

Sense-organs.—The *eyes* have the same essential structure as the compound eye of Apus. The chitinous cuticle covering the distal end of the eye-stalk is transparent, is divided by delicate lines into square areas or *facets*, and constitutes the *cornea*. Beneath each facet of the cornea is an ommatidium, optically separated from its neighbours by black pigment, and consisting of an outer segment or *vitreous body*, and an inner segment or *retinula*, formed of sensory cells enclosing a rhabdome.

The antennules contain two sense-organs, to which have been assigned the functions of smell and balance respectively. The *olfactory organ* is constituted by a number of extremely delicate *olfactory setæ*, borne on the external flagellum, and supplied by branches of the antennulary nerve. The so-called *statocyst* is a

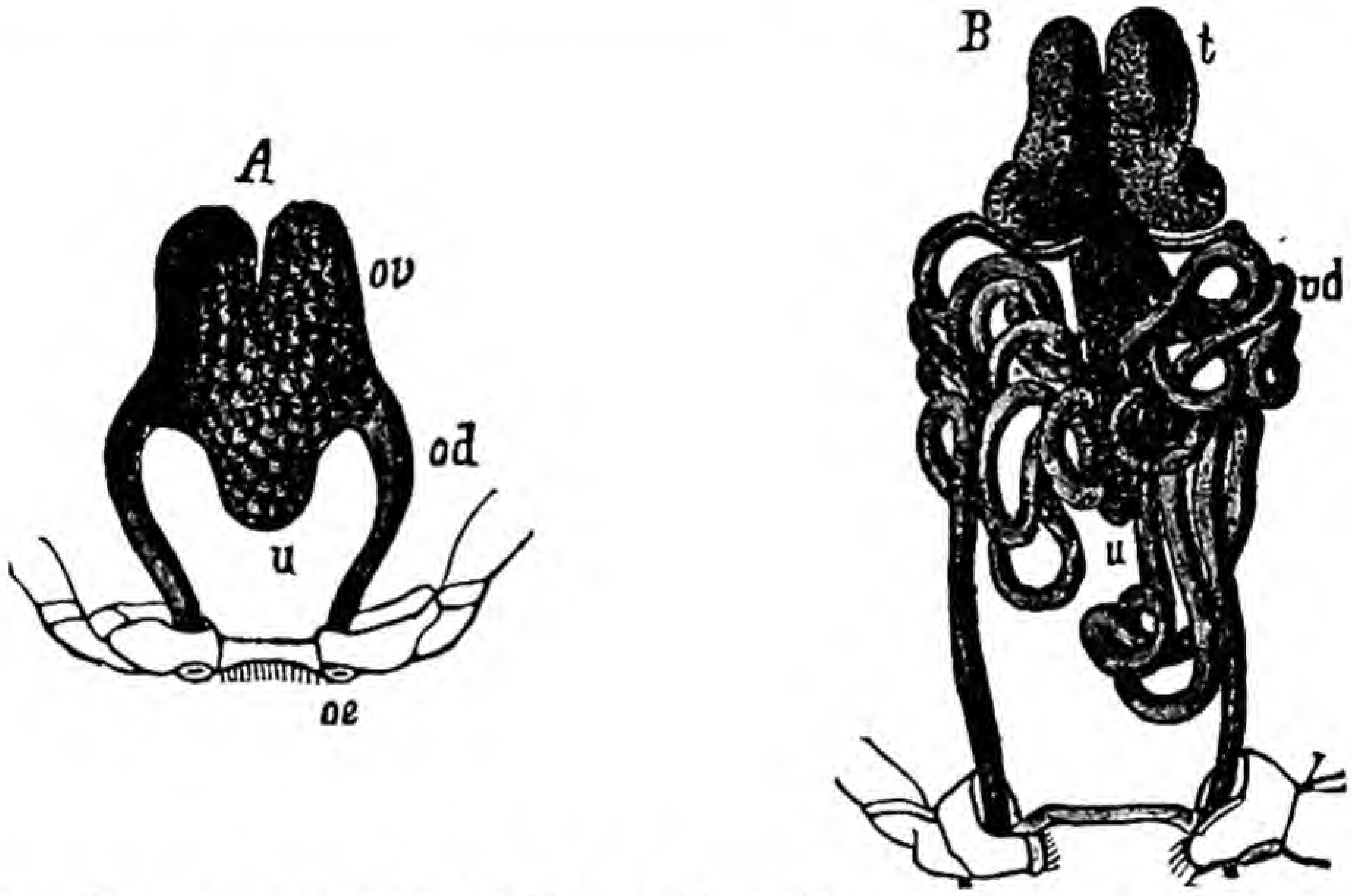


FIG. 375.—Reproductive organs of **Astacus fluviatilis.** *A*, female; *B*, male. *od.* oviduct; *oe*, its external opening; *ov.* ovary; *t.* testis; *u*, unpaired posterior portion of gonad; *vd.* vas deferens. (From Lang's *Comparative Anatomy*, after Huxley.)

sac formed by invagination of the dorsal surface of the proximal segment, and is in free communication with the surrounding water by a small aperture. The chitinous lining of the sac is produced into delicate feathered *sensory setæ*, supplied by branches of the antennulary nerve; and in the water which fills the sac are minute sand-grains, which take the place of *statoliths*, but, instead of being formed by the animal itself, are taken in after each ecdysis, when the lining of the sac is shed. Changes in the animal's position in space bring about corresponding changes in the direction of the pressure of the statoliths upon the sensory setæ and are thus signalled to those parts of the central nervous system which govern the co-ordination of limb movements. Many of the setæ on the body generally have a definite nerve-supply, and are probably *tactile organs*.

Reproduction.—The Crayfish is diœcious, and presents a very obvious

sexual dimorphism. The abdomen of the female is much broader than that of the male: the first and second pleopods of the male are modified into tubular or rather spout-like copulatory organs (Fig. 366, 9); and the reproductive aperture is situated in the male on the proximal podomere of the fifth leg, in the female on that of the third.

The *testis* (Fig. 375, *B*, *t*, *u*) lies in the thorax, just beneath the floor of the pericardial sinus, and consists of paired anterior lobes (*t*) and an unpaired posterior lobe (*u*). From each side goes off a convoluted *vas deferens* (*vd.*), which opens on the proximal segment of the last leg. The *sperms* are curious amœboid bodies produced into a number of stiff processes or pseudopodia (Fig. 24, *f*): they are aggregated into vermicelli-like *spermatophores* by a secretion of the vas deferens.

The *ovary* (*A*, *ov.*, *u*) is also a three-lobed body, and is similarly situated to the testis: from each side proceeds a thin-walled *oviduct* (*od.*), which passes downwards, without convolutions, to open on the proximal segment of the

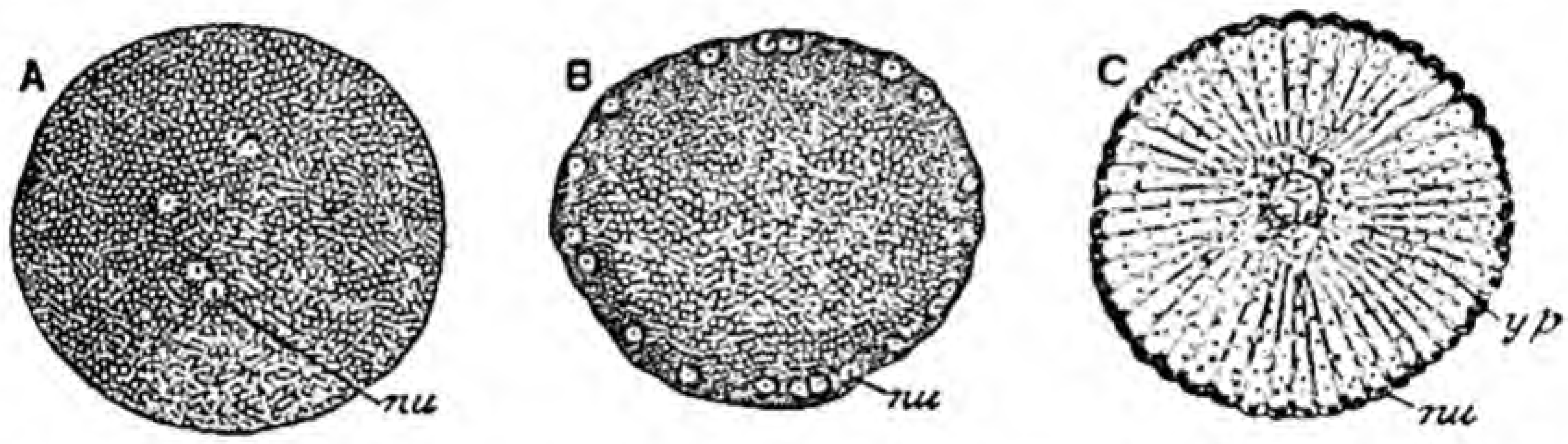


FIG. 376.—Three stages in the formation of the blastoderm of **Astacus fluviatilis**, *nu.* nuclei; *yp.* yolk-pyramids. (From Korschelt and Heider, after Morin and Reichenbach.)

third or antepenultimate leg. The eggs are of considerable size and are centrolecithal.

As in Apus, both ovary and testis are hollow organs, discharging their products internally. The ova, when laid, are fastened to the setæ on the pleopods of the female by the sticky secretion of glands occurring both on those appendages and on the segments themselves: they are fertilized immediately after laying, the male depositing spermatophores on the ventral surface of the female's body just before oviposition.

Development.—The process of *cleavage of the fertilized egg* presents certain striking peculiarities. The nucleus (Fig. 376, *A*, *nu.*) divides repeatedly, but no corresponding division of the protoplasm takes place, with the result that the morula-stage, instead of being a heap of cells, is multinucleate but non-cellular. Soon the nuclei thus formed retreat from the centre of the embryo, and arrange themselves in a single layer close to the surface (*B*): around each of these protoplasm accumulates, the central part of the embryo consisting entirely of yolk-material. We thus get a *superficial cleavage*, characterized by a central mass of yolk and a superficial layer of cells collectively known as the *blastoderm* (*C*). Subsequently the yolk itself undergoes a process of

cleavage, becoming divided into radiating *yolk pyramids* (*y.p.*), each with its base in contact with one of the cells of the blastoderm and its apex pointing to the centre of the egg: before long, however, these pyramids fuse into an undivided mass of yolk.

The first indications of the future Crayfish take the form of thickenings on what will become the ventral surface. There are at first five of these thickenings—two anterior, the *head-lobes* (Fig. 377, *c. l.*), on which the eyes subsequently appear; two somewhat further back, the *thoracico-abdominal rudiments* (*th. abd.*); and one, posterior and unpaired, the *endoderm-disc* (*inv.*). On the latter an invagination of the blastoderm takes place, giving rise to a small sac, the *archenteron*, which communicates with the exterior by an aper-

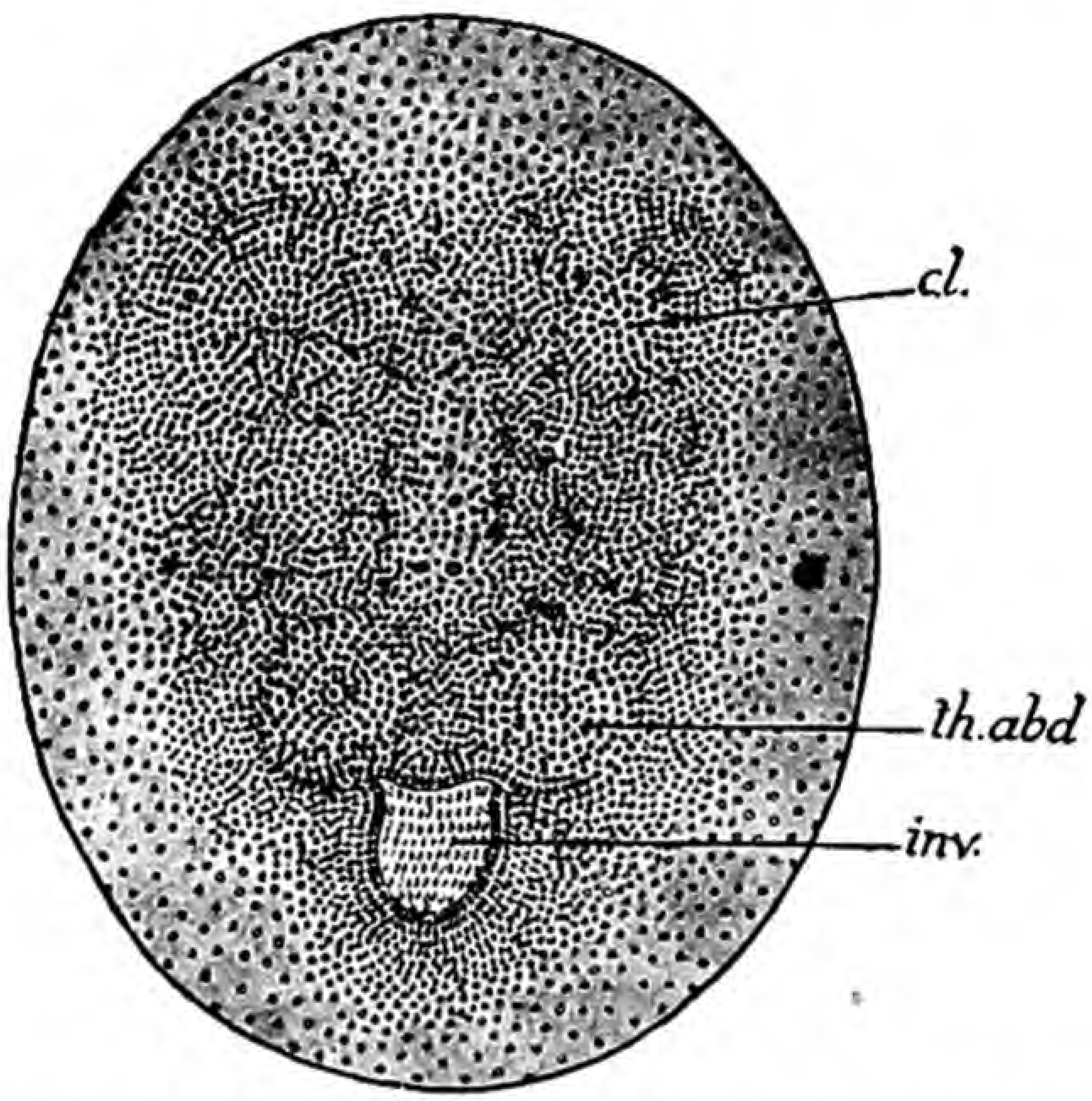


FIG. 377.—Ventral view of an embryo of **Astacus fluviatilis**, gastrula stage, in order to show the ventral plate. *c. l.* cephalic lobe; *inv.* invaginated area of blastoderm (endoderm disc); *th. abd.* thoracico abdominal rudiments. (From MacBride, after Reichenbach.)

ture, the *blastopore*. By this process the embryo passes into the *gastrula-stage*, which, however, differs from the corresponding stage in the types previously studied in the immense quantity of food-yolk filling up the space (blastocœle) between ectoderm and endoderm. Very soon the embryo becomes triploblastic, or three-layered, by the budding off of cells from the endoderm in the neighbourhood of the blastopore: these accumulate between the ectoderm and endoderm, and constitute the mesoderm.

Before long the blastopore closes, converting the archenteron into a shut sac (Fig. 379, *A*): the thoracico-abdominal rudiments unite with one another, forming a well-marked oval elevation (Fig. 378, *th. abd.*), and three pairs of elevations appear between it and the head-lobes. These are the rudiments of

the first three pairs of appendages, the antennules (at^1.), antennae (at^2.), and mandibles (*mn.*) : by their appearance the embryo passes into the *nauplius-stage*, which in this case is passed through in the egg, instead of being active and free-swimming as in Apus.

Between the bases of the antennules and antennæ a pit appears, which soon deepens and widens : this is the *stomodæum* (Fig. 379, *stdm.*), and its aperture the mouth. A similar but narrower and more cylindrical pit appears on the thoracico-abdominal rudiment : this is the *proctodæum* (*pcdm.*), and its aperture the anus. For a considerable time both stomodæum and proctodæum remain

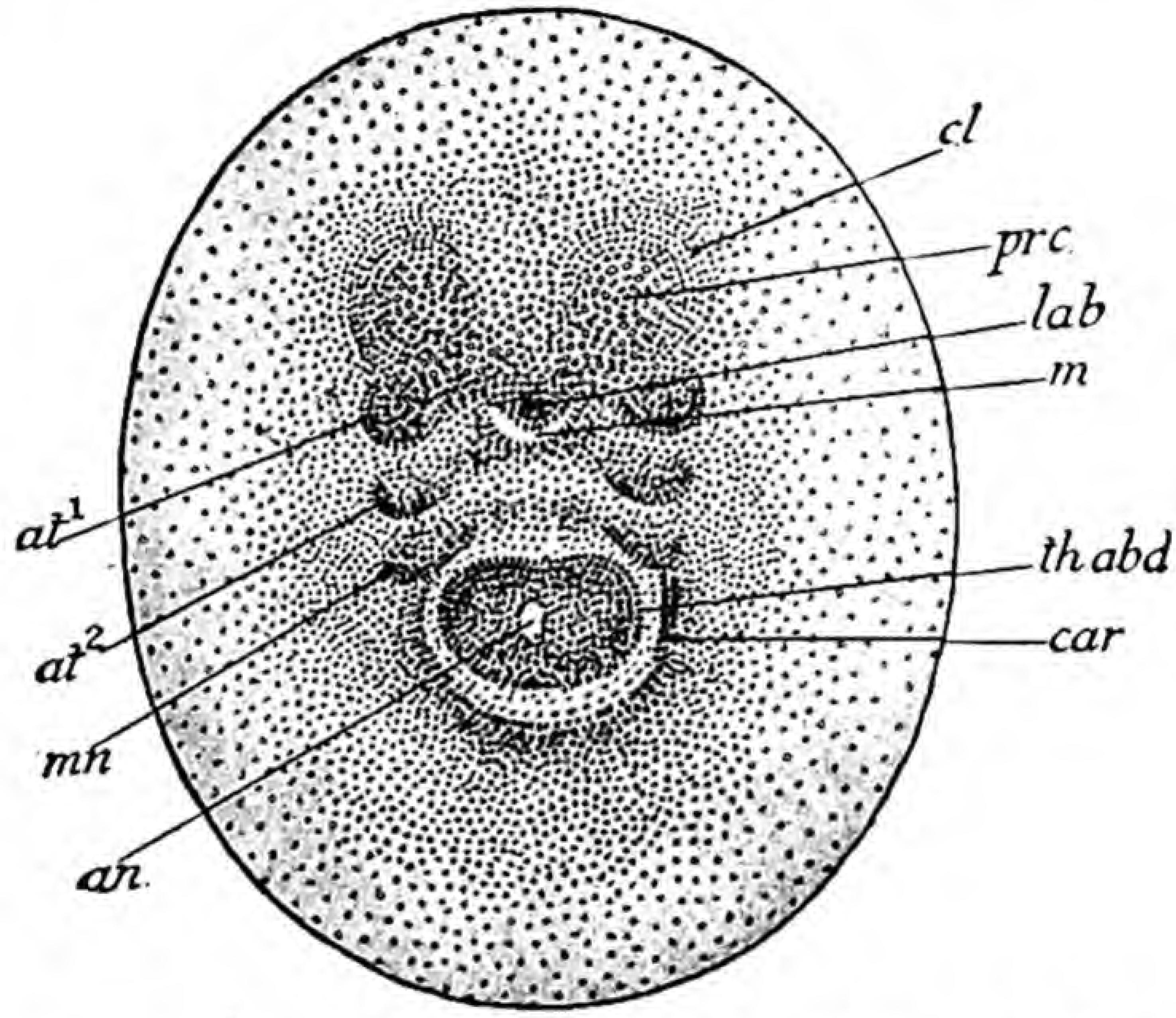


FIG. 378.—" Nauplius stage " in the development of **Astacus fluviatilis** viewed from the ventral side. *an.* anus; at^1. rudiment of antennule; at^2. rudiment of antenna; *car.* ridge marking the first trace of the carapace; *c. l.* cephalic lobe; *lab.* labrum; *m.* mouth; *mn.* rudiment of mandible; *pr. c.* proto-cerebrum; *th. abd.* thoracico-abdominal rudiment. (From MacBride, after Reichenbach.)

in the condition of blind sacs, but after a time they open into the archenteron, a complete enteric canal being thus constituted. In the meantime the endoderm cells lining the archenteron grow outwards in a radial direction, ingesting the yolk as they do so, until they take the form of long columns, in contact by their outer ends with the ectoderm (Fig. 379, *B*).

The thoracico-abdominal rudiment soon begins to increase rapidly in length, but, being enclosed in the egg-membranes, it grows not backwards but forwards, being in fact folded upon the anterior part of the body in much the same way as the abdomen of the adult during extreme flexion.

In the meantime the post-mandibular appendages are formed in regular order from before backwards : the eye-stalks appear (Fig. 380, *oc.*), as well as

the labrum (*lab.*), and a fold on each side of the thorax, which is the rudiment of the carapace (*car.*), and this gradually extends dorsally until it meets with its fellow of the opposite side and covers in the cephalothorax. The embryo now consists of a nearly globular cephalothorax with a small abdomen and a nearly complete set of appendages, all tucked in under the cephalothorax and closely

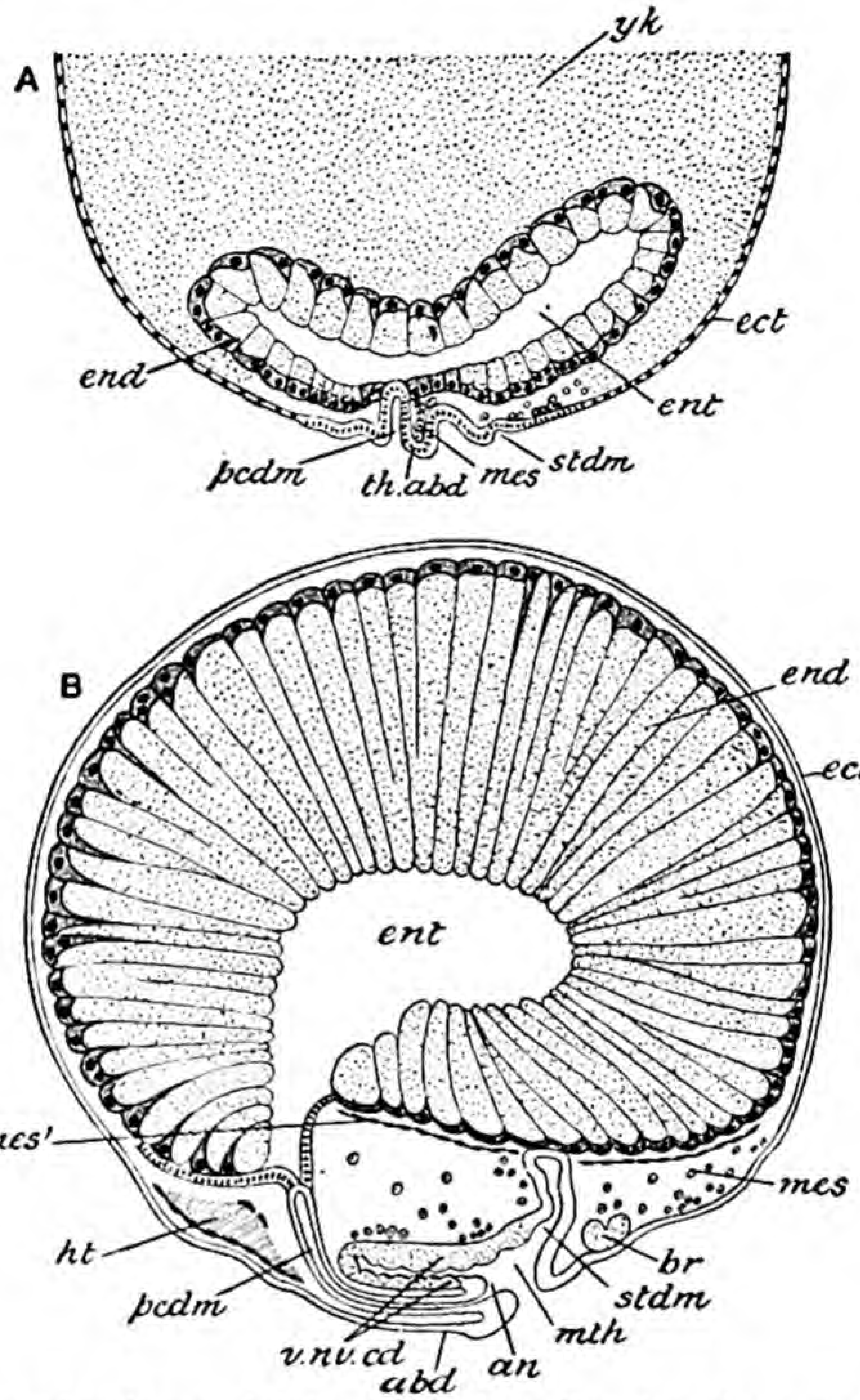


FIG. 379.—Sections of embryos of **Astacus.** *A*, Nauplius-stage (compare Fig. 378); *B*, after development of thoracic appendages (*cf.* Fig. 380). *abd.* abdomen; *an.* anus; *br.* brain; *ect.* ectoderm; *end.* endoderm; *ent.* enteron; *ht.* heart; *mes.* mesoderm; *mes*[1]. splanchnic layer of mesoderm; *mth.* mouth; *pcdm.* proctodæum; *stdm.* stomodæum; *th. abd.* thoracico-abdominal rudiment; *v. nv. cd.* ventral nerve-cord. (From Korschelt and Heider, after Reichenbach.)

packed together within the egg-membranes. In this condition the embryo is hatched, and for some time clings to the pleopods of the mother or to the empty egg-shells by means of the peculiarly hooked chelæ of its first pair of legs, and is attached also by a bundle of threads secreted along the posterior border of the larval telson.

The development of the principal internal organs must be referred to very briefly. From the ectoderm arise not only the epidermis of the adult, but the epithelium of the gullet and stomach and of the hind-gut, the epithelium of the

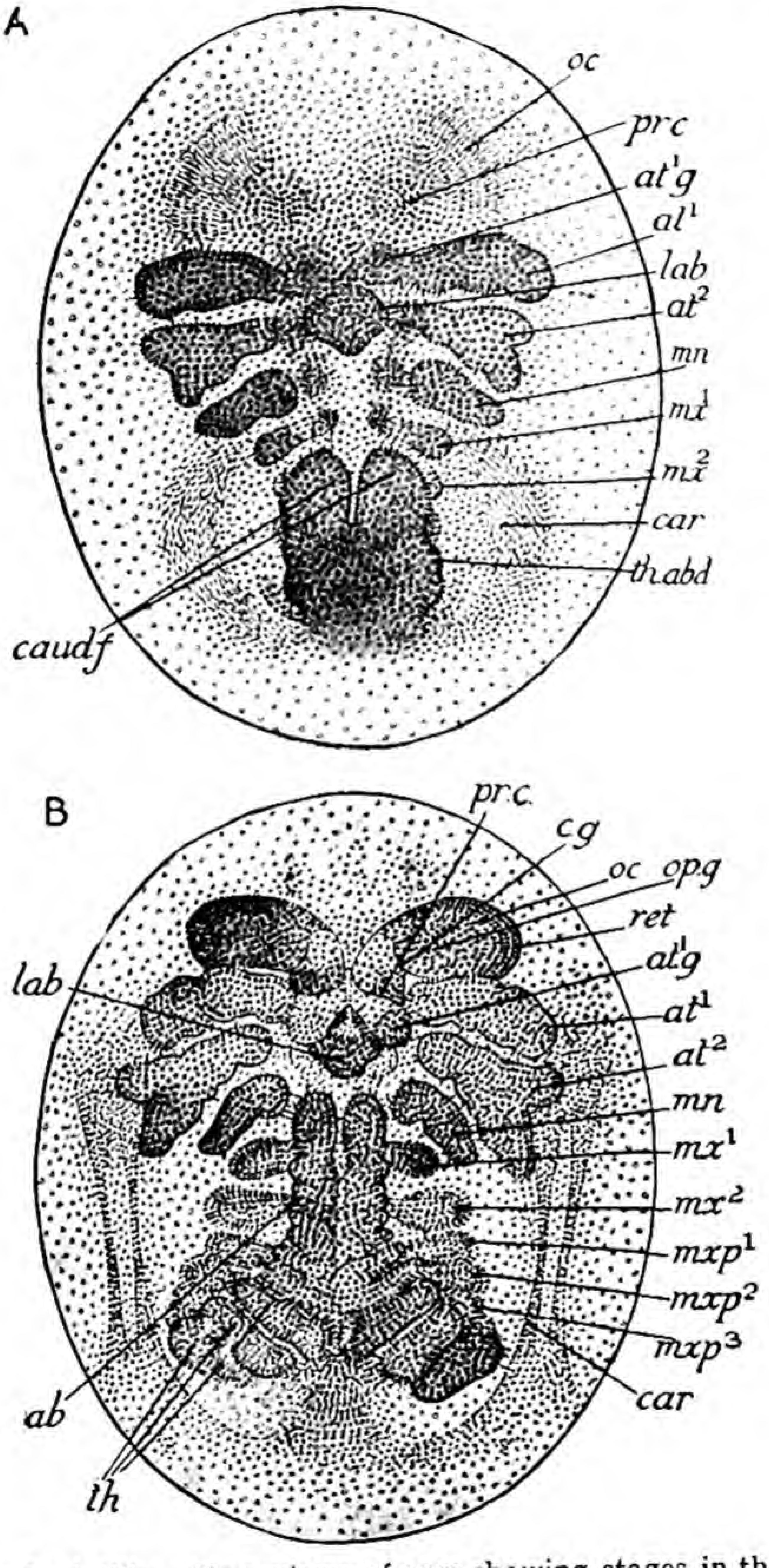


FIG. 380.—**Astacus fluviatilis.** Two views of eggs showing stages in the development of the appendages. *A*, stage in which the rudiments of maxillæ have appeared and in which the abdomen has become forked. *B*, stage in which the rudiments of thoracic appendages are appearing and in which the abdomen is segmented. *ab.* abdomen; *at*¹. antennule; *at*². antenna; *at*¹*g.* antennulary ganglion; *car.* fold which becomes edge of the carapace; *caud. f.* forked extremity of abdomen; *c.g.* cerebral groove which gives rise to the optic ganglion; *lab.* labrum; *mn.* mandible; *mx*¹. first maxilla; *mx*². second maxilla; *mxp*¹. *mxp*². *mxp.*³ maxillipedes; *oc.* eye-stalk; *op. g.* optic ganglion; *pr. c.* protocerebrum; *ret.* retinulæ; *th.* rudiments of thoracic appendages. (From MacBride, after Reichenbach.)

gills, the nervous system, the vitreous cells and retinulæ of the eyes, and the epithelium of the statocyst. From the endoderm arises the epithelium of the mid-gut and of the digestive glands, the latter being formed as tubular branching outgrowths of the archenteron. The connective-tissues, the muscles, the vascular system, the gonads, and at least part of the kidneys, are all of mesodermal origin.

2. Distinctive Characters and Classification.

The Crustacea are Arthropods in which the six anterior segments are fused with the pre-segmental region to form the head, while the rest are usually divisible into two regions, the thorax and the abdomen. More or fewer of the thoracic segments may be fused with the head to form a cephalothorax. The head may bear a median eye, which frequently disappears in the adult, and a pair of compound eyes. The latter frequently become elevated on jointed eye-stalks. The appendages of the head are (1) *the antennules, which are considered as belonging to the second metamere;* (2) *the antennæ, which are certainly post-oral or metameric appendages shifted forwards to a pre-oral position;* (3) *the mandibles or crushing jaws;* (4) *the first maxillæ; and* (5) *the second maxillæ. The thoracic and abdominal appendages are variously modified as jaws, legs, fins, or accessory reproductive organs. With the exception of the antennules, the appendages are typically biramous, consisting of a stem or protopodite bearing two branches, the endopodite and exopodite.*

The body is covered externally by a chitinous cuticle, which becomes thickened and sometimes calcified in regions where no movement is required, forming a series of hard parts or sclerites, *separated by flexible chitin; the whole chitinous cuticle thus constitutes an exoskeleton. Typically there is one sclerite to each metamere behind the head, and to each podomere in the appendages, but concrescence of sclerites frequently takes place. The exoskeleton is produced into setæ, which are hollow processes of the cuticle containing prolongations of the underlying epidermis.*

Respiration takes place either by the general surface of the body or by gills, which are hollow offshoots of the thoracic wall or of the thoracic or abdominal limbs. The stomodæum and proctodæum form a considerable portion of the enteric canal, and are lined with chitin: the mesenteron gives rise to digestive glands. The body-cavity is divided into compartments, most of which contain blood and are portions of the vascular system: the true cœlome may be represented by compartments of the body-cavity not containing blood and by the cavities of the reproductive organs. There is a vascular system which nearly always includes a contractile heart, formed as a muscular dilatation of a dorsal vessel, and communicating by valvular ostia with an enclosing pericardial sinus. The blood is taken from the heart to the various organs by arteries, and is returned to the pericardial sinus by sinuses and veins: the respiratory organs are interposed in the returning current. The renal organs are peculiarly modified cœlomoducts,

which may take the form either of shell-glands opening on the second maxillæ, or of antennary (green) glands opening on the antennæ.

The nervous system consists of a brain united by œsophageal connectives with a ventral nerve-cord, formed of a double chain of glanglia joined together by commissures and connectives. The first four pairs of embryonic ganglia commonly unite to form the brain, which is therefore a syn-cerebrum. The sexes are separate or united: sexual dimorphism is common: parthenogenesis frequently occurs. The sperms are either amœboid with radiating stiff processes or pseudopodia, or flagellate: the eggs are usually centrolecithal, but may be telolecithal, or almost alecithal. The muscles are striped, and there are no cilia.

Cleavage of the egg is usually superficial, but may be complete or discoid. The embryo very usually has a distinct nauplius-stage, which may be a free-swimming larva or may be passed through before hatching, and is characterized by the presence of three pairs of appendages which become the antennules, antennæ, and mandibles of the adult.

The Crustacea are classified as follows:—

Sub-class I.—Branchiopoda.

Crustacea with a varying number of body-segments, provided with appendages of a uniform character, usually foliaceous, rarely leg-like, the posterior region (abdomen) devoid of appendages and provided with a pair of many-jointed or unjointed caudal styles. A cephalic carapace is sometimes absent: when present it may be either shield-like or bivalve. Paired eyes are usually present. The antennules and the maxillæ are reduced or absent: the mandibles devoid of, or with a vestigial, palp. The larva is a nauplius or metanauplius.

Order 1.—Anostraca.

Branchiopoda in which a carapace is not developed. The eyes are stalked: the antennæ are prehensile in the male, reduced in the female. The appendages of the body-segments number 11, 17, or 19 pairs. The caudal styles are not jointed.

This order includes *Branchipus* (Fig. 381), *Chirocephalus*, and *Artemia*.

Order 2.—Notostraca.

Branchiopoda in which there is a large dorsal shield-shaped carapace. The eyes are sessile. The antennæ are reduced. There are 40 to 63 pairs of trunk appendages. The caudal styles are many-jointed.

Including *Apus* and *Lepidurus* (Figs. 353 and 354).

ORDER 3.—CONCHOSTRACA.

Branchiopoda with a carapace divided into two lateral portions or valves like the shell of a bivalve mollusc, and enclosing the entire animal. The antennæ are biramous and are used as swimming appendages. The eyes are sessile, coalescent. The appendages of the body-segments number 10 to 32 pairs. The caudal styles are in the form of unjointed, curved claws.

Including *Cyzicus* (*Estheria*), *Lynceus*, *Limnetis* (Fig. 381), and one or two other genera.

ORDER 4.—CLADOCERA.

Branchiopoda of small size with a bivalved carapace which encloses the trunk but not the head. The eyes are sessile and united together. The antennæ are biramous and used as swimming appendages. Only 4 to 6 trunk appendages; caudal styles unjointed, claw-like.

To this order belong *Sida*, *Daphnia*, *Polyphemus*, *Leptodora* (Fig. 382), etc.

Sub-class II.—Ostracoda.

Crustacea with unsegmented or indistinctly segmented body bearing not more than four pairs of appendages on the trunk, the limbless posterior part provided with a pair of caudal styles. There is a well-developed bivalved carapace. Paired eyes may be present or absent. Both antennules and antennæ are used in swimming; the latter are generally biramous. The mandibles have a palp. The young escapes from the egg as a nauplius.

In this sub-class are comprised *Cypris*, *Cythere*, etc. (Fig. 383).

Sub-class III.—Copepoda.

Crustacea with elongated, distinctly segmented body, bearing usually five pairs of limbs, the last four having the character of biramous swimming appendages, sometimes with a sixth pair which may be vestigial: the posterior region (abdomen) without appendages, provided with a pair of caudal styles. The cephalic dorsal shield is not extended backwards, but usually coalesces with the exoskeleton of the first (and sometimes also the second) body-segment. Paired eyes are absent except in the Branchiura. Both antennules and antennæ are usually well developed, and the latter are sometimes biramous: they may both be used as swimming organs or for prehension. The mandibles may be provided with a palp. The genital apertures are situated on the seventh body-segment. The young is a nauplius. In the parasitic forms more or fewer of these general characteristics may become lost in the adult.

In this group are included (*a*) free-swimming forms, such as *Cyclops* (Water-flea) (Fig. 384), and (*b*) parasitic forms or Fish-lice—*e.g.*, *Ergasilus*, *Chondracanthus*, *Lernæa* (Fig. 385).

Sub-class IV.—Branchiura.

Parasitic Crustacea with compound eyes and a suctorial mouth. Some of the appendages of the body-segments are usually provided with peculiar appendages—the *flagella*. The genital apertures are situated on the fifth body-segment. This sub-class includes the Carp-lice, *Argulus* (Fig. 386), and two other genera.

Sub-class V.—Cirripedia.

Imperfectly segmented Crustacea, which are always fixed in the adult condition, and may be parasitic. There are usually six pairs of biramous cirriform appendages of the body region. The limbless posterior region (abdomen) is rudimentary, and is usually provided with a pair of caudal styles. The carapace forms a pair of folds, the mantle, completely enclosing the animal, and usually supported by a system of calcareous plates giving rise to a hard shell. Paired eyes are absent in the adult. The antennules of the larva give rise to organs of attachment and become vestigial in the adult: the antennæ usually disappear. The mandibles have no palp. The sexes are united in the great majority. The young animal is hatched in the nauplius form and passes later through a stage—the *cypris* stage—in which it is provided with a bivalved shell.

Order 1.—Thoracica.

Non-parasitic Cirripedia, permanently fixed in the adult condition, with six pairs of biramous trunk appendages.

Including *Lepas* (Goose Barnacle) (Fig. 387) and *Balanus* (Acorn Barnacle) (Fig. 388).

Order 2.—Acrothoracica.

Sessile Cirripedia boring in the shells of Molluscs; with fewer than six pairs of trunk appendages.

Including *Alcippe* (living in the shell of Whelks).

Order 3.—Ascothoracica.

Parasitic Cirripedia, generally with six pairs of trunk appendages; mouth appendages modified into piercing and sucking organs. Parasitic in Anthozoa and Echinodermata.

Including *Petrarca* (living in Hexacorallia).

Order 4.—Apoda.

Parasitic Cirripedia without mantle and without trunk appendages; body maggot-like.

Only representative: *Proteolepas* (living in the stalked Barnacle *Alepas*).

ORDER 5.—RHIZOCEPHALA.

Parasitic Cirripedia in which the body has undergone extreme degeneration, and has lost all trace of appendages and of alimentary canal in the adult condition.

Including *Sacculina* (Fig. 389) and *Peltogaster*.

Sub-class VI.—Malacostraca.

Crustacea in which the body is always distinctly segmented and is made up in all cases except the Leptostraca of an anterior region (thorax) of eight segments, and a posterior (abdomen) of six, rarely seven, with a terminal tail-piece or telson—the total number of segments, leaving the pre-segmental region and the teslon out of account, being twenty (twenty-one in the Leptostraca). The appendages of the thorax and abdomen are sharply marked off from one another. The abdomen is devoid of caudal styles. The exoskeleton of the head united with that of more or fewer of the thoracic segments to form a cephalothoracic carapace. Paired eyes are usually present and may be sessile or stalked. The antennules are biramous in most cases. The mandibles are provided with a palp. There is usually a metamorphosis, but a nauplius-stage rarely occurs.

Series I.—Leptostraca (Phyllocarida).

Malacostraca in which the abdomen contains seven segments and a telson—the last segment devoid of appendages, the telson bearing a pair of caudal styles. There is a large bivalved carapace with an adductor muscle, enclosing the greater part of the body. The thoracic appendages are foliaceous, the abdominal biramous.

Includes only one order, the Nebaliacea, with *Nebalia* (Fig. 390) and three allied genera.

Series II.—Eumalacostraca.

Malacostraca with six segments and a telson in the abdomen, the latter never provided with caudal styles. Carapace never bivalve. Thoracic appendages nearly always leg-like, but seldom all uniform : their protopodite always made up of two podomeres except in the Stomatopoda.

Division 1.—Syncarida.

Eumalacostraca devoid of carapace, with the first thoracic segment united with the head or marked off from it by a groove. Heart elongated, tubular.

ORDER ANASPIDACEA.

Syncarida in which the thoracic appendages are provided (except the last or the last two) with exopodites, and (except the last) with a double series of

lamellar epipodites (gills). The abdominal appendages, except the first two in the male and the last in both sexes, have the endopodite reduced or absent. The last pair of abdominal appendages (uropods) are expanded, forming with the telson a fan-like tail-fin. This, the only order of the Syncarida, comprises the genera *Anaspides*, *Koonunga*, and *Paranaspides* (Fig. 391). A related form is *Bathynella*, which, however, has only one pair of abdominal appendages and no tail-fin.

Division 2.—Peracarida.

Eumalacostraca in which the carapace, when present, leaves at least four of the thoracic segments free. Heart elongated, tubular.

Order 1.—Mysidacea.

Peracarida in which, though the carapace extends over the greater part of the thorax, it does not coalesce dorsally with more than the first three segments. The eyes, when present, are supported on movable stalks; the antennules are biramous, and the antennæ have a scale-like exopodite or squame. The first pair of thoracic appendages are specialized as maxillipedes. The thoracic appendages (except sometimes the first and second pairs) are biramous. The uropods with the telson form a broad fan-like tail-fin.

This order includes *Mysis* (Fig. 392), *Lophogaster*, and other genera.

Order 2.—Cumacea.

Peracarida in which the carapace coalesces with the first three or four segments of the thorax, is produced on each side to enclose a branchial cavity, and in front is drawn out into a rostrum. The eyes usually coalesce into one, which is not borne on a movable stalk. The antennules are sometimes biramous; the antennæ have no exopodites. Some of the thoracic appendages are biramous. The telson may coalesce with the last segment of the abdomen. The uropods are styliform, and there is no fan-like tail-fin.

Includes *Cuma* (*Bodotria*), *Diastylis* (Fig. 393), etc.

Order 3.—Tanaidacea.

Peracarida in which the carapace coalesces with the first two thoracic segments and is produced on each side to enclose a branchial cavity. The eyes, when present, are usually supported on short stalks which are not movable. The antennules are sometimes biramous: the antennæ may possess small exopodites. The first pair of thoracic limbs are modified as maxillipedes. The second and third thoracic limbs sometimes have vestigial exopodites. The uropods are usually narrow.

This order includes *Apseudes*, *Tanais*, *Leptochelia*, etc.

Order 4.—Isopoda.

Peracarida in which the dorsal exoskeleton of the head is not produced into a carapace, but in which the first and sometimes also the second segment of the thorax coalesce with the head. The eyes are sessile or borne on short processes which are not movable. The antennules are nearly always uniramous: the antennæ sometimes bear a minute exopodite. The thoracic limbs have no exopodites: the first pair are modified as maxillipedes; the rest are usually alike in character. The abdominal appendages are usually biramous; the rami function as branchiæ. The body is nearly always dorso-ventrally compressed. This is a large order including many families, *e.g.*—*Anthura*, *Asellus*, *Phreatoicus*, *Oniscus*, *Idotea*, *Sphæroma*, *Bopyrus*, *Gyge* (Figs. 395, 397).

Order 5.—Amphipoda.

Peracarida with the characters of the preceding order, except that (1) the body is nearly always laterally compressed; (2) the second and third pairs of thoracic appendages are nearly always modified as prehensile organs (gnathopods); (3) there are vesicular or lamellar branchiæ attached to the bases of more or fewer of the thoracic limbs; (4) the abdominal appendages are distinguishable into two sets, the three anterior pairs with many-jointed rami, the three posterior (including the uropods) with unjointed styliform rami.

Includes *Orchestia* (Fig. 404), *Gammarus* (Fig. 394), *Hyperia*, *Caprella*, *Cyamus* (Fig. 396), and many other genera.

Division 3.—Eucarida.

Eumalacostraca in which the carapace coalesces with all the thoracic segments, forming a cephalothorax. The eyes are borne on movable stalks. The heart is short, sac-like, and situated in the thorax.

Order 1.—Euphausiacea.

Eucarida in which none of the thoracic limbs take the form of maxillipedes; with a single series of branchiæ (podobranchs) attached to the bases of the thoracic limbs. The larva is a nauplius.

This is a comparatively small order of pelagic Eumalacostraca, including *Euphausia* (Fig. 405), *Thysanopoda*, *Nyctiphanes*, and a few other genera.

Order 2.—Decapoda.

Eucarida in which the first three pairs of thoracic appendages are modified as maxillipedes, with the branchiæ usually in several series—podobranchs, arthrobranchs, and pleurobranchs.

Sub-order a.—*Macrura.*

Decapoda with well-developed, elongated abdomen, which is usually held in the extended position, and terminates in an expanded fan-like tail-fin composed of the telson and the uropods. The eyes are not enclosed in orbits. The antennules and antennæ are both large; the former are not sunk in pits, and the antennæ usually have a scale-like exopodite (squame).

Included among the Macrura are (*a*) swimming forms—*Penæus* and *Palæmon* (Prawns), *Crangon* (Shrimps), *Lucifer*, etc.; and (*b*) creeping forms—*Homarus* (Lobster), *Astacus* (*Potamobius*), *Astacopsis*, *Paranephrops*, *Cambarus* (Fresh-water Crayfishes), *Palinurus* (Rock-lobsters), *Scyllarus*, etc. (Figs. 398, 399).

Sub-order b.—*Anomura.*

Decapoda with the abdomen more or less reduced, usually held in a flexed position, and not provided with such a well-developed tail-fin as in the Macrura.

In most respects the Anomura are intermediate between the Macrura and the Brachyura. Examples are the Hermit-crabs—*Eupagurus* (Fig. 400) and other genera, the Cocoa-nut crab—*Birgus*, *Galathea*, *Hippa*, *Porcellana*, etc.

Sub-order c.—*Brachyura.*

Decapoda in which the abdomen is greatly reduced, shorter than the cephalothorax, and permanently flexed beneath it. The antennules and the eyes are both capable of being retracted into cavities. There is a metamorphosis comprising *zoœa* and *megalopa* stages.

Including the true Crabs such as *Cancer*, *Maia*, *Grapsus*, etc. (Figs. 401, 402).

Division 4.—Hoplocarida.

Eumalacostraca in which the carapace does not coalesce with at least the last four thoracic segments, so that the cephalothorax is relatively short. In front of the head proper are two movable segments, one bearing the stalked eyes, the other the antennules. The branchiæ are borne on the abdominal appendages. The heart is elongated. There is a metamorphosis, but a nauplius stage is not known to occur.

ORDER I.—STOMATOPODA.

This, the only order of Hoplocarida, includes *Squilla* (Fig. 403), *Gonodactylus*, and other genera.

3. General Organization.

There is no class in the animal kingdom which presents so wide a range of organization as the Crustacea, or in which the deviations in structure from the "type-form" are so striking and so interesting from their obvious adaptation to the mode of life.

The most interesting modifications are those connected with the **external characters** and the **structure of the appendages.** As we have seen, the body consists of a pre-segmental region, a variable number of metameres, and an

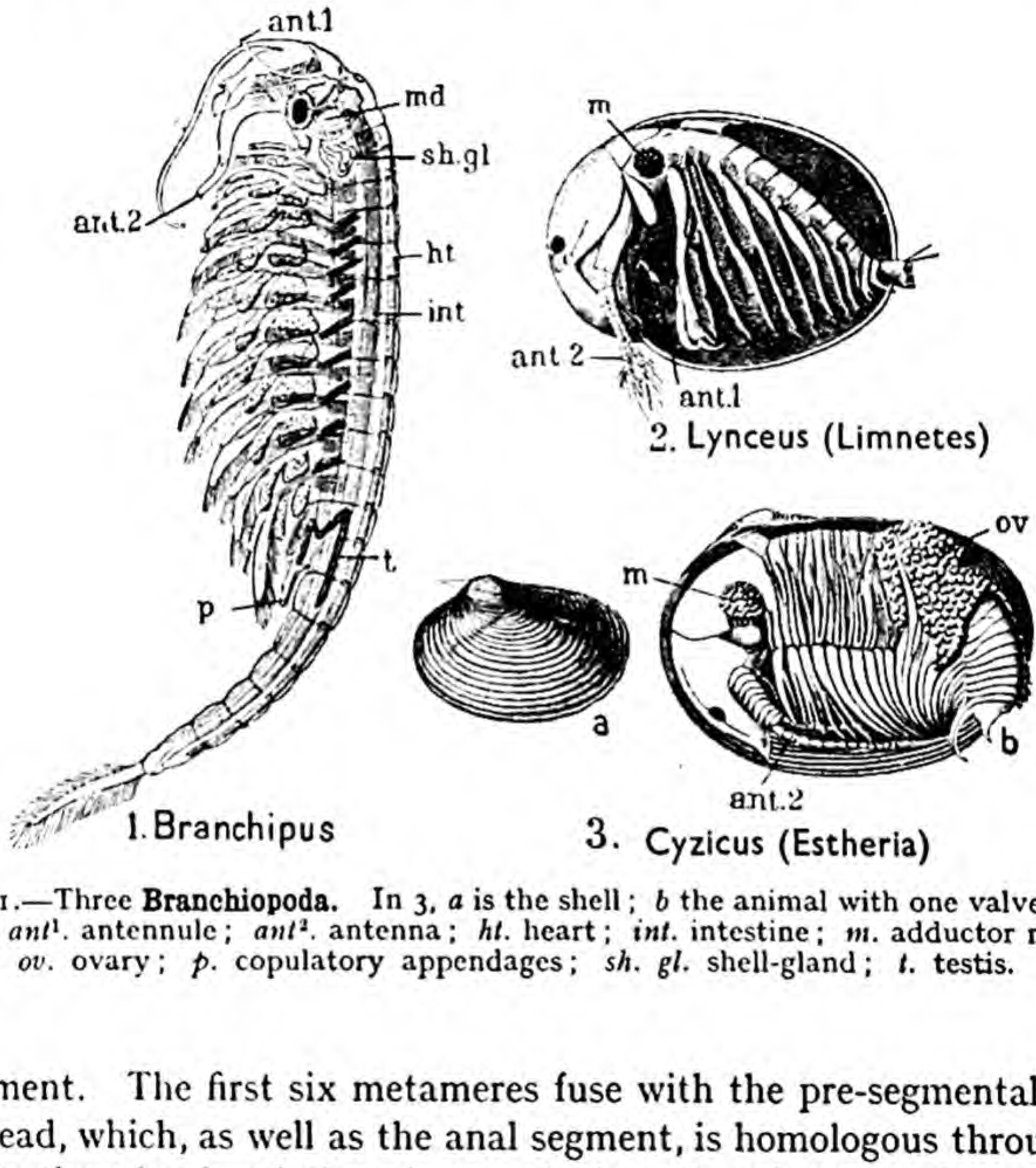


FIG. 381.—Three **Branchiopoda.** In 3, *a* is the shell; *b* the animal with one valve of the shell removed. *ant*[1]. antennule; *ant*[2]. antenna; *ht.* heart; *int.* intestine; *m.* adductor muscle; *md.* mandible; *ov.* ovary; *p.* copulatory appendages; *sh. gl.* shell-gland; *t.* testis. (After Gerstaecker.)

anal segment. The first six metameres fuse with the pre-segmental region to form a head, which, as well as the anal segment, is homologous throughout the class. On the other hand, there is no strict homology between the various post-cephalic metameres in different forms until we come to the Malacostraca, in which their number is constant.

There is considerable diversity of form among the *Branchiopoda*. Apus has already been described. Branchipus (Fig. 381, 1) and Artemia (the Brine-shrimp) (*Anostraca*) are small shrimp-like forms, the former living in fresh-water lakes, the latter in brine-pools; they have no carapace, and the eyes are raised on unjointed stalks. In Lynceus (Limnetis) (2), on the other hand,

and in Cyzicus (Estheria) (3) (*Conchostraca*) the carapace takes the form of a *shell*, formed of two parts or *valves*, united in Cyzicus by a hinge, and resembling the shell of a cockle or other bivalved mollusc. The limbs have the same general structure as those of Apus, but the antennæ are often of considerable size, and are sometimes modified into prehensile organs.

In the *Cladocera*, of which the common fresh-water Daphnia (Fig. 382, 1) is a good example, there is a great reduction in size (1–2 mm.), and a corresponding shortening of the body by a reduction in the number of metameres. Segmentation is very imperfect, and the whole body, but not the head, is covered

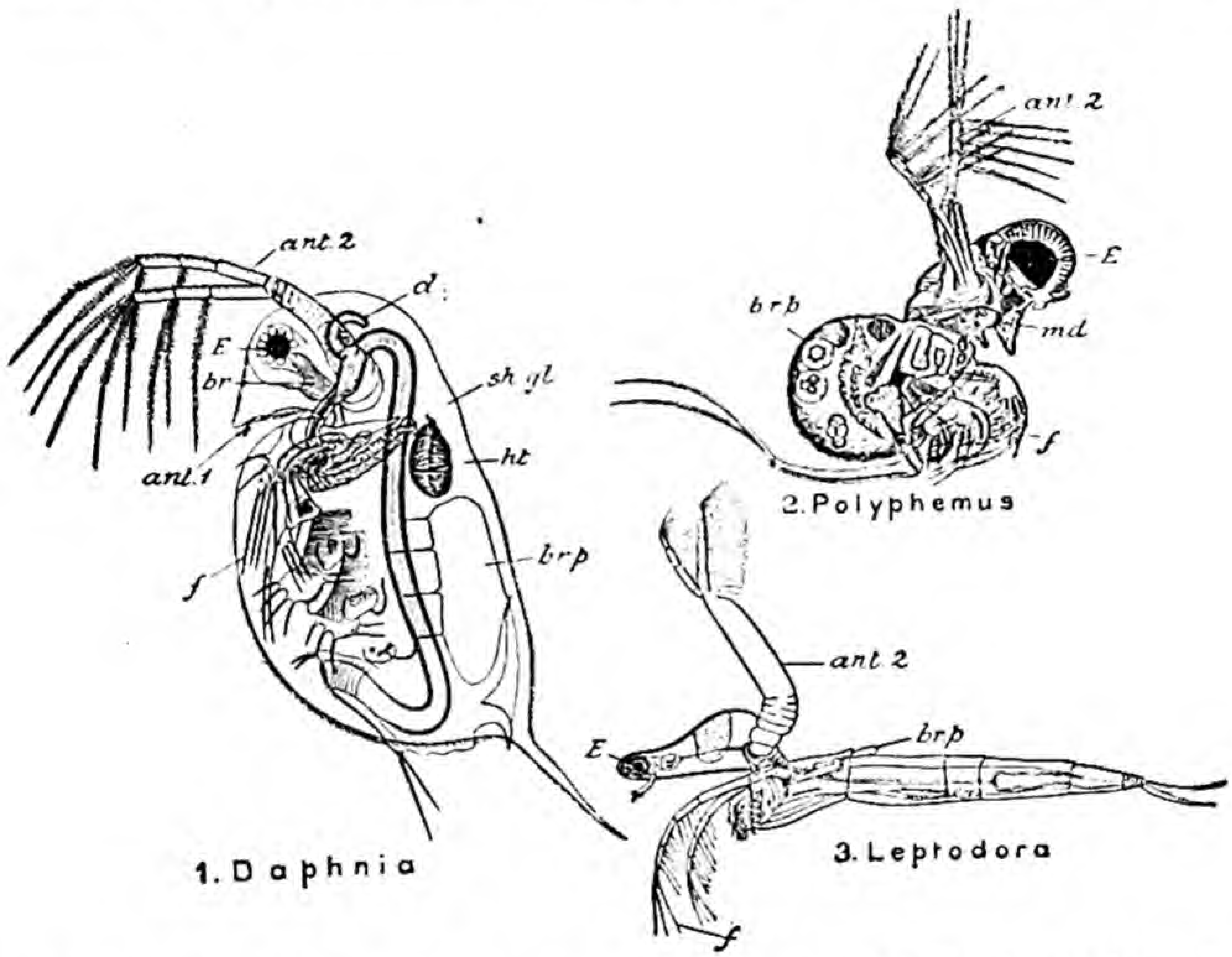


FIG. 382.—Three **Cladocera.** *ant. 1*, antennule; *ant. 2*, antenna; *br.* brain; *br. p.* brood-pouch; *E.* eye; *d. gl.* digestive gland; *f.* swimming feet; *ht.* heart; *md.* mandible; *sh. gl.* shell-gland. (1 after Claus, 2 and 3 after Gerstaecker.)

by a large, folded carapace. The abdomen is turned downwards and is in constant movement, sweeping out any foreign particles which may have made their way among the feet. Between the abdomen of the female and the posterior part of the carapace is a large *brood-pouch* (*br.p.*), in which the eggs are stored. The paired eyes (*E*) have fused into a single organ, which exhibits a constant trembling movement. The antennules (*ant. 1*) are small, the antennæ (*ant. 2*) very large, biramous, and constitute the chief organs of locomotion. The mandibles are large, the second maxillæ absent in the adult, and there are usually five pairs of leaf-like swimming-feet (*f*) on the thorax. The abdomen is devoid of appendages. Many of the Cladocera have an extraordinarily

grotesque form (2, 3), owing to the peculiar shape of the head, the immense antennæ, and the great hump-like brood-pouch.

The *Ostracoda* are usually not more than 1–2 mm. in length, and are found both in fresh- and sea-water. One of the commonest genera is *Cypris*, which occurs in immense numbers in stagnant pools. *Cythere* is a common marine form.

The body (Fig. 383) is unsegmented, and is completely enclosed in a carapace (*A*), the right and left halves of which are articulated together along the dorsal edge so as to form a bivalved shell (*C*), which may be variously ornamental or sculptured. The valves are opened by the elasticity of a ligament, which passes

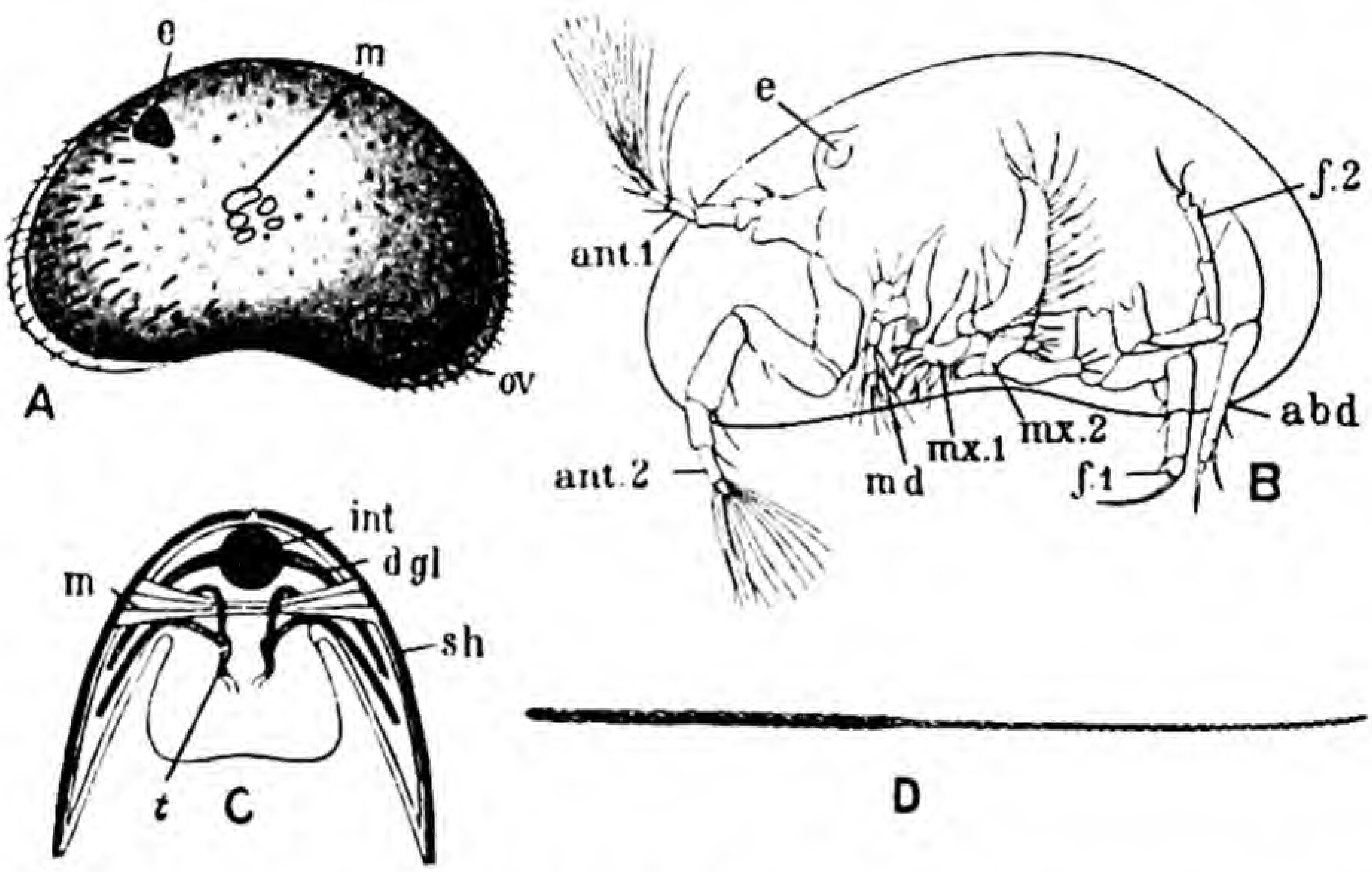


FIG. 383.—*A*, external view of **Cypris**; *B*, the same with the appendages exposed by the removal of the left valve of the shell; *C*, transverse section; *D*, a single sperm. *abd.* abdomen; *ant. 1*, antennule; *ant. 2*, antenna; *d. gl.* digestive gland; *e.* median eye; *f. 1*, *f. 2*, thoracic feet; *int.* intestine; *m.* abductor muscle; *md.* mandible; *mx. 1*, *mx. 2*, maxillæ; *ov.* ovary; *sh.* shell; *t.* testis. (After Gerstaecker and Zenker.)

from one to another at the hinge, and are closed by a large *adductor muscle* (*m.*), which extends transversely from valve to valve, its insertions giving rise to markings on the shell (*A*, *m.*), often of systematic value.

At the anterior end is a median eye (*e*), and in some forms compound eyes are present as well. There are only seven pairs of appendages. The antennules (*ant. 1*) and antennæ (*ant. 2*) are large, and the latter usually biramous. The mandible (*md.*) has a large leg-like palp and a flabellum-like offshoot. The first maxilla (*mx. 1*) also bears a large plate resembling a flabellum of Apus. The last cephalic appendage (second maxilla, *mx. 2*) is jaw-like in some forms (*Cypris*), leg-like in others (*Cythere*). The only thoracic appendages are two or four pairs of slender legs (*f. 1*, *f. 2*). The abdomen (*abd.*) is devoid of appendages, and is terminated by a pair of small caudal styles.

The diversity of form among the *Copepoda* is so great that it will be advisable to consider separately the *free-swimming* and the *parasitic Copepoda.*

[illegible] *free-swimming Copepoda* are well represented by the common water-flea [illegible]), found everywhere in fresh and brackish water, and easily recognizable,

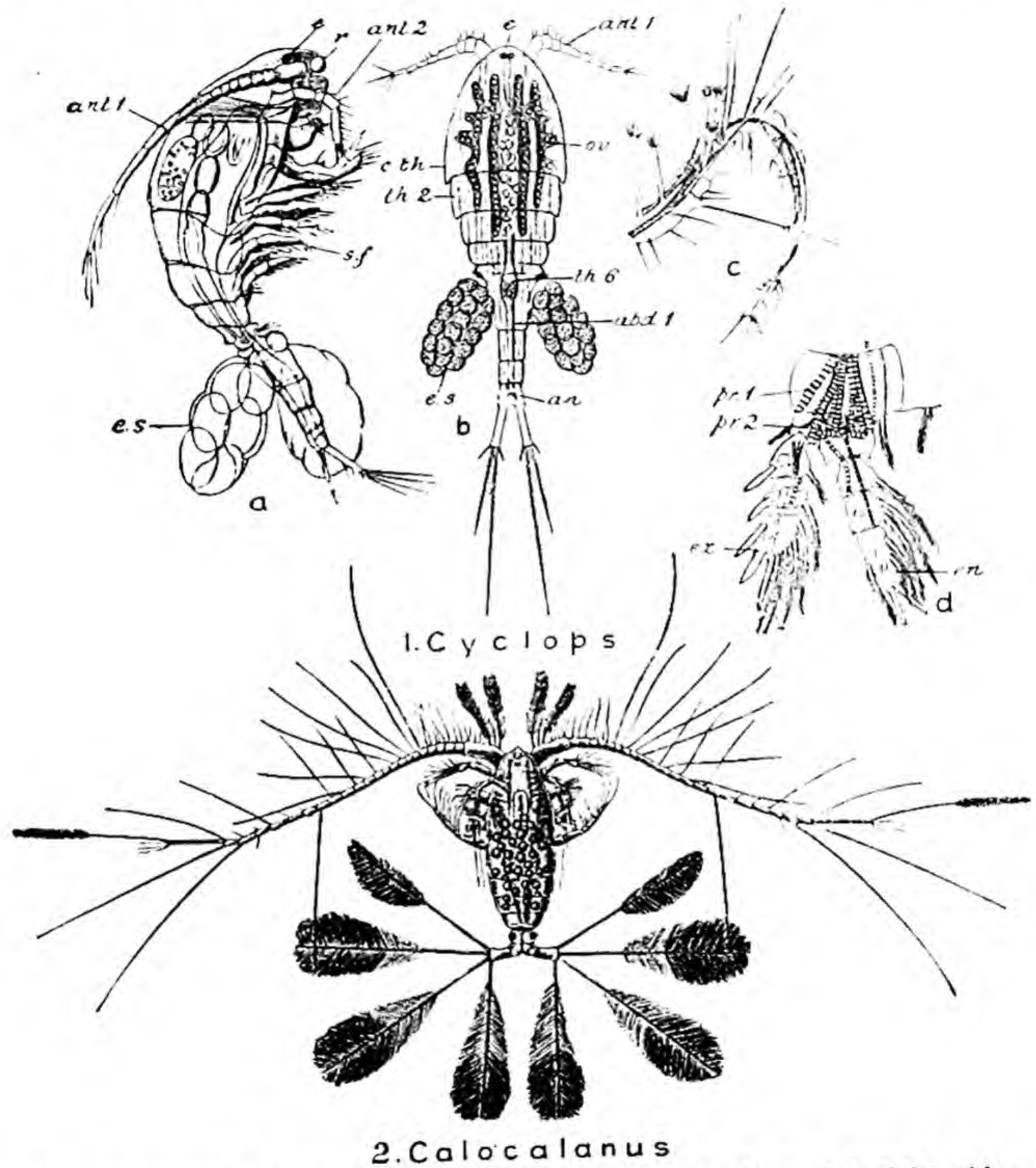


FIG. 384.—Free-swimming **Copepoda.** 1*a* female **Cyclops,** from the right side; *b.* dorsal view; *c.* antenna of male; *d.* swimming-foot. *abd.* 1, first abdominal segment; *an.* anus; *ant.* 1, antennule; *ant.* 2, antenna; *c. th.* cephalothorax; *e.* median eye; *en.* endopodite; *e. s.* egg-sac; *ex.* exopodite; *ov.* ovary; *pr.* 1, *pr.* 2, protopodite; *r.* rostrum; *s. f.* swimming-feet; *th.* 2, *th.* 6, thoracic segments. (After Huxley, Gerstaecker, Hartog, and Giesbrecht.)

in spite of its minute size, by its elongated form, its rapid, jerky movements, and by the egg-sacs of the female.

Cyclops (Fig. 384, 1) has been compared in form to a split pear, the broad end being anterior, and the convex surface dorsal. The first thoracic segment is fused with the head, and the cephalothorax (*c. th.*) thus formed is covered with

a carapace produced in front into a short spine or *rostrum* (*r*), near the base of which, on the dorsal surface, is the median eye (*e*). There are five free thoracic segments : the last (*th. 6*) bears the genital aperture, and is fused in the female

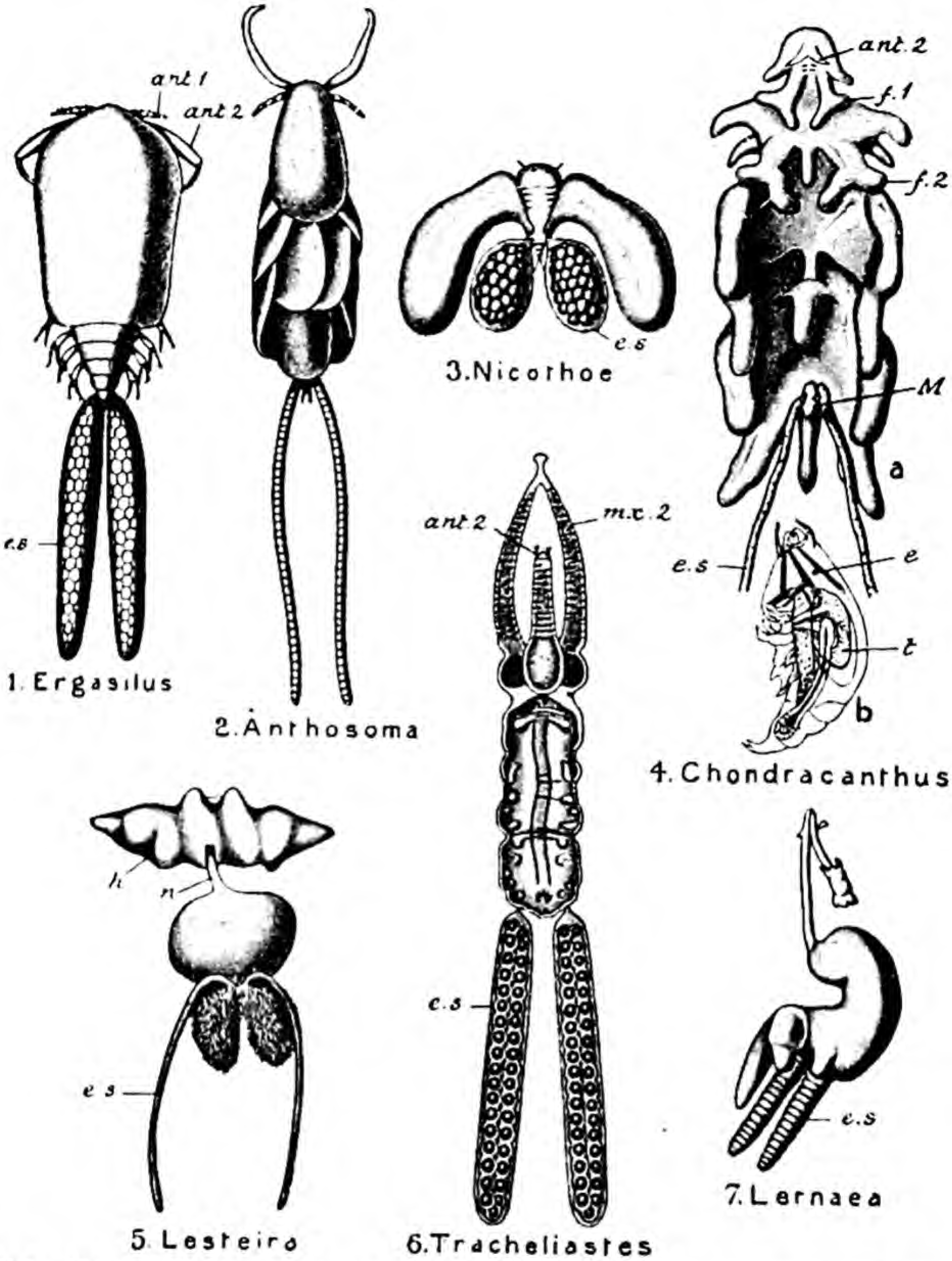


FIG. 385.—Various forms of parasitic **Copepoda.** 4a, female; 4b, male. *ant. 1*, antennule; *ant. 2*, antenna; *e.* median eye; *e. s.* egg-sac; *f. 1*, *f. 2*, thoracic feet; *h.* head; *M.* male; *mx. 2*, second maxillæ; *n.* "neck." (After Gerstaecker, Claus, Cuvier, and G. M. Thompson.)

with the first abdominal segment (*abd. 1*). There are four abdominal segments : the last bears the dorsal anus (*an.*), and a pair of caudal styles produced into plummed setæ.

The antennules (*ant. 1*) are very large, and are the principal organs of

locomotion. In the male they are modified (*c*)—by a peculiar form of joint and long setæ—as clasping organs, used for holding the female during copulation. The antennæ (*ant. 2*) are comparatively short and uniramous. Mandibles and maxillæ are present, and the first four thoracic segments bear biramous swimming-feet (*1a, s.f.*), those of the right and left sides being connected by transverse plates or *couplers*. The fifth thoracic segment bears a pair of vestigial limbs: the abdominal segments are limbless.

Some of the pelagic marine *Copepoda* (Fig. 384, 2) are remarkable for their brilliant colours and for the extraordinary development of their setæ, especially those of the caudal styles.

The *parasitic Copepoda*, or Fish-lice, present a very interesting series of modifications, illustrating the degeneration of structure which so often accompanies parasitism. *Ergasilus* (Fig. 385, 1) is found on the gills of the Bass (*Morone labrax*); it is readily recognizable as a Copepod, but the appendages are greatly reduced, the antennæ modified into hooks for holding on to the host, and the eyes absent. *Anthosoma* (2), found in the mouth of the Porbeagle Shark (*Lamna cornubica*), has recognizable appendages, but the form of the body is much modified by the development of curious overlapping lobes. *Nicothöe* (3), found on the gills of the Lobster, has antennæ and mouth-parts modified for suction: the abdomen is normal, but the thorax is produced into huge lobes, which give it a curiously deformed appearance. In *Chondracanthus* (4), the various species of which are parasites on the gills of Bony Fishes, there is, at the first glance, nothing to suggest that the animal is a Crustacean, except the characteristic copepod egg-sacs: the body is depressed, unsegmented, and produced into crinkled lobes, and it requires careful examination to discover that antennules, hooked antennae (*ant. 2*)—used for attachment—mandibles, maxillæ, and two pairs of legs (*f.1, f.2*) are present. The male (*b*) is of higher organization than the female, but of minute size—about $\frac{1}{12}$ the length of its mate—and is permanently attached to her body, close to the genital aperture (*a, M*). In *Lernæa* (7) and its allies the body is vermiform with a curiously lobed anterior end: the maxillæ are adapted for piercing the skin of the host and sucking its juices, and there are minute vestiges of feet. In *Lesteira* (5) the degradation is even more marked: the female reaches a large size—70 mm. in length, excluding the egg-sacs—and is found with the swollen head between the skin and flesh of a fish (*Genypterus blacodes*), and the rest of the body hanging freely into the water. Lastly, in *Tracheliastes* (6) the second maxillæ (*mx. 2*) are greatly enlarged, and form a characteristic organ of attachment.

Argulus (Fig. 386) is the most familiar example of the *Branchiura*, or Carp-lice. It is an external parasite on fresh-water Fishes (Carp, Stickleback, etc.), not permanently attached like the degenerate forms just described, but crawling freely over the surface of the host. The body consists of an oval flattened cephalothorax, and a small bilobed

abdomen (*ab.*). The mandibles and maxillæ are piercing organs enclosed in a sucking-tube or proboscis (*r.*), in front of which is a median tube ending in a spine (*st.*). The second maxillæ are divided into two portions, the anterior of which (*kf. 1*) are modified into sucking-discs by which the parasite clings to the surface of its host, and there are four pairs of swimming-feet (b_1—b_4).

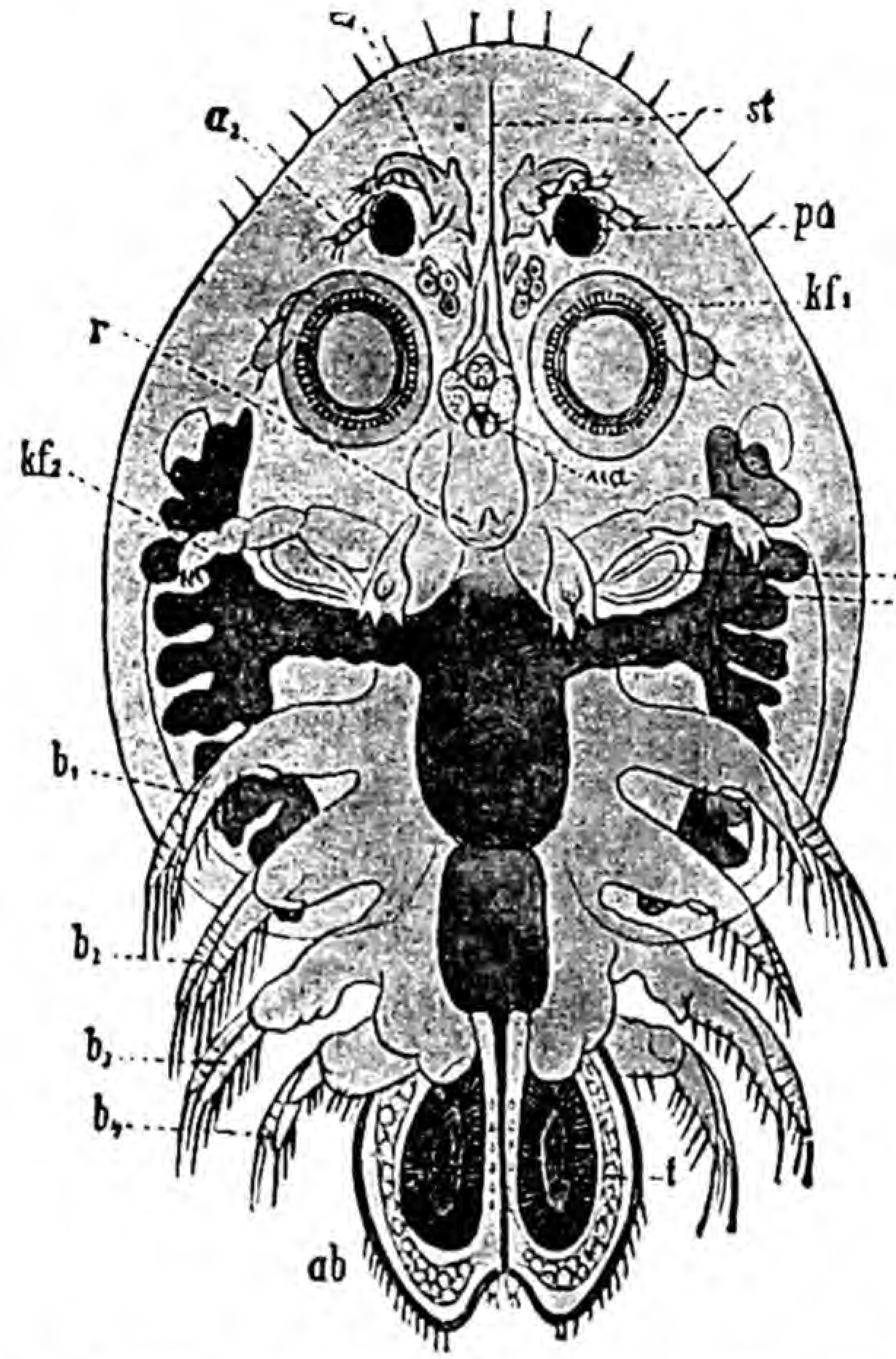


FIG. 386.—**Argulus foliaceus,** young male. a_1, antennule; a_2, antenna; *ab.* abdomen; b_1—b_4, thoracic feet; *d.* digestive glands connected with intestine; *kf. 1*, anterior or suctorial feet; *kf. 2*, posterior or leg-like portion of second maxillæ; *pa.* paired eye; *r.* rostrum; *sd.* shell-gland; *st.* stylet; *ts.* testis; *ua.* median eye. (From Lang's *Comparative Anatomy.*)

The most familiar examples of the *Cirripedia* are the Barnacles found on ships' bottoms, piles, etc., and the Acorn-shells or Sessile Barnacles which occur in immense numbers on rocks between tide-marks in all parts of the world.

The Common Goose Barnacle (*Lepas anatifera*) is attached by a long stalk or peduncle (Fig. 387, *A*, *ped.*), covered with a wrinkled skin, and bearing at its distal end the body proper enclosed in a sort of bivalved carapace, formed by a fold of the skin, and strengthened by five calcareous plates. Of these one is median and dorsal, and is called the *carina* (*c*); two are lateral and proximal, the *scuta* (*s*); and two lateral and distal, the *terga* (*t*). During life the carapace is partly open, and from the ventrally placed aperture delicate setose filaments

are protruded and keep up a constant grasping movement: these are the endo- and exo-podites of the biramous thoracic limbs, of which there are six pairs. Removal of the carapace shows the feet to arise from a vermiform unsegmented body (*B*), attached on the ventral aspect to the stalk and carapace by its anterior end, while its posterior end is free and terminates in a long filament, the penis (*p*), immediately dorsal to which is the anus. The mouth is ventral and

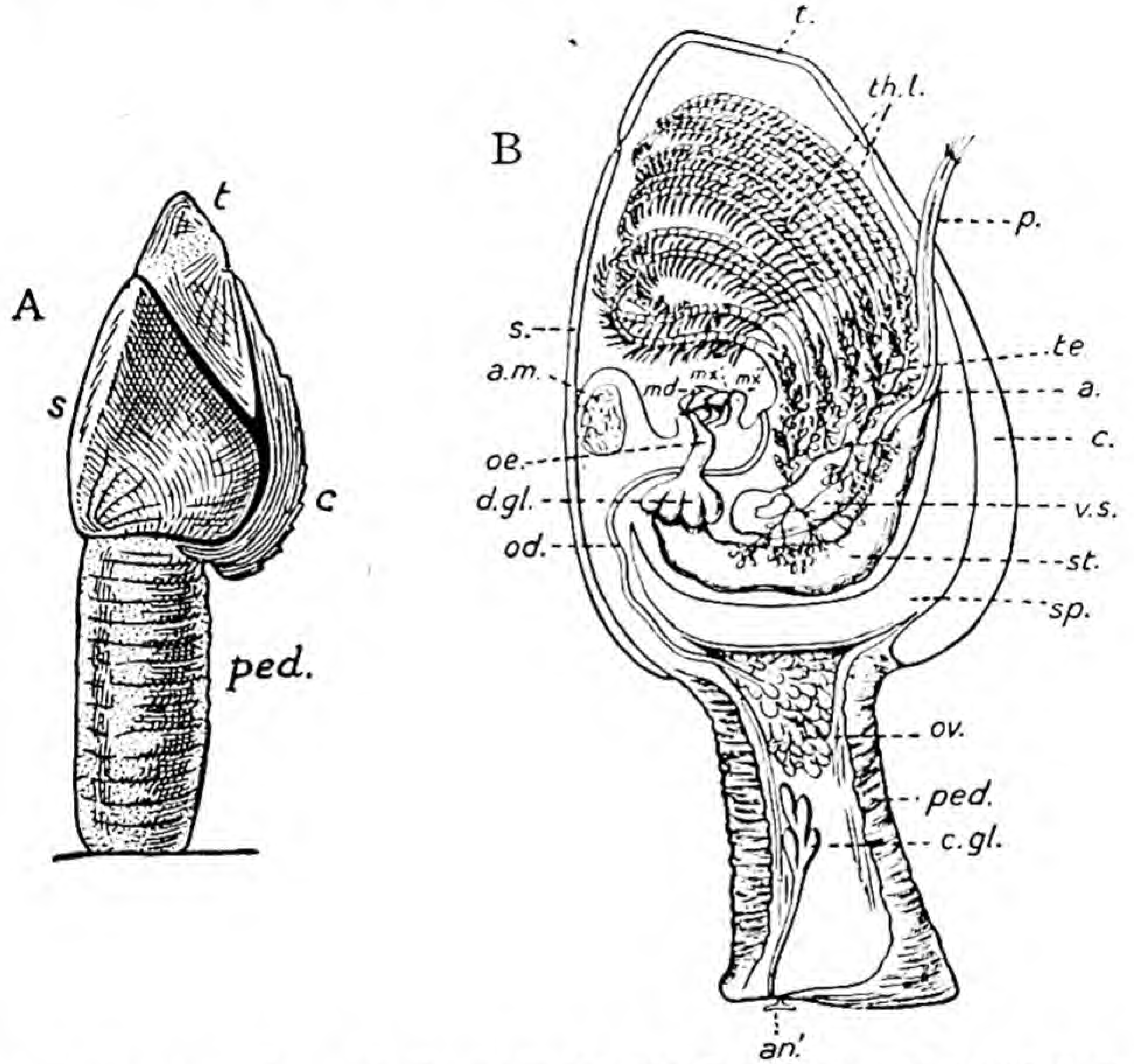


FIG. 387.—**Lepas anatifera.** *A*, the entire animal; *B*, anatomy. *a.* anus; *a. m.* adductor muscle; *an'.* antennule; *c.* carina; *c. gl.* cement gland; *d. gl.* digestive gland; *md.* mandible; *mx'.* first maxilla; *mx''.* second maxilla; *od.* oviduct; *œ.* œsophagus; *ov.* ovary; *p.* penis; *ped.* peduncle (stalk); *s.* scutum; *sp.* space between carapace and the body; *st.* stomach; *t.* tergum; *te.* testis; *th. l.* thoracic limbs; *v. s.* vesicula seminalis. (From Shipley and MacBride's *Zoology*. University Press, Cambridge.)

anterior, and is provided with a pair of mandibles (*md.*) and two pairs of maxillæ (*mx'.*, *mx''.*). There are no antennæ; at first sight the antennules appear to be absent, but a careful examination shows the presence of a pair of minute structures (*an'.*) on the proximal or attached surface of the stalk, and embedded in the cement by which the animal is fixed to its support; these are the antennules, and their position relatively to the mandibles shows that the stalk is formed by an elongation of the anterior region of the head.

The Sessile Barnacles or Acorn-shells (*Balanus*) have no stalk (Fig. 388), the head-region being short and broad. The scuta (*s*) and terga (*t*) support a

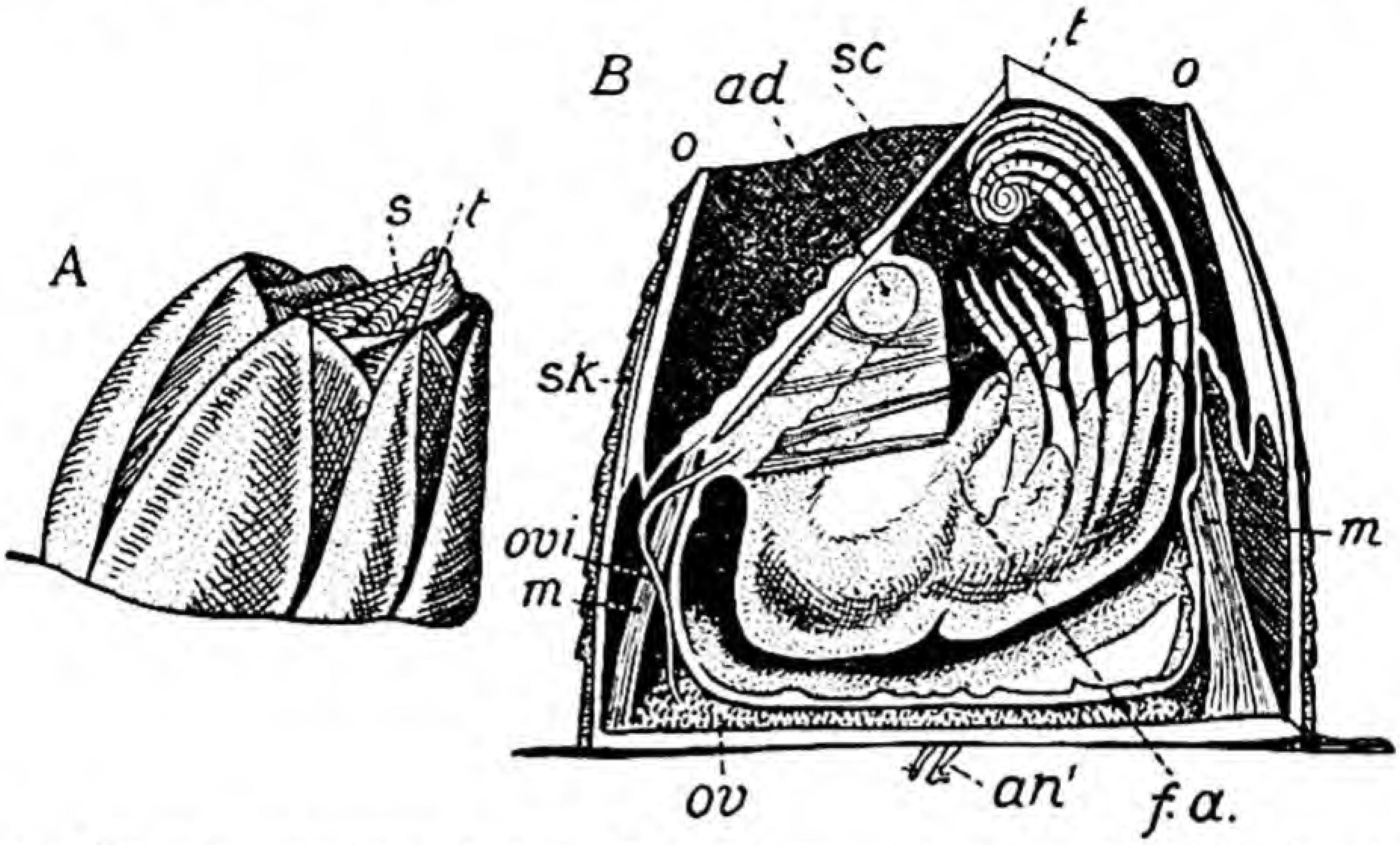


FIG. 388.—**Balanus.** *A*, external view; *B*, anatomy. *an'*. antennules; *ad*. adductor muscle; *m*. muscles of scuta and terga; *o*. edge of parapet; *ov*. ovary; *ovi*. oviduct; *s*., *sc*. scutum; *sk*. parapet; *t*. tergum; *f.a*. female aperture. (From Lang's *Comparative Anatomy*, after Darwin.)

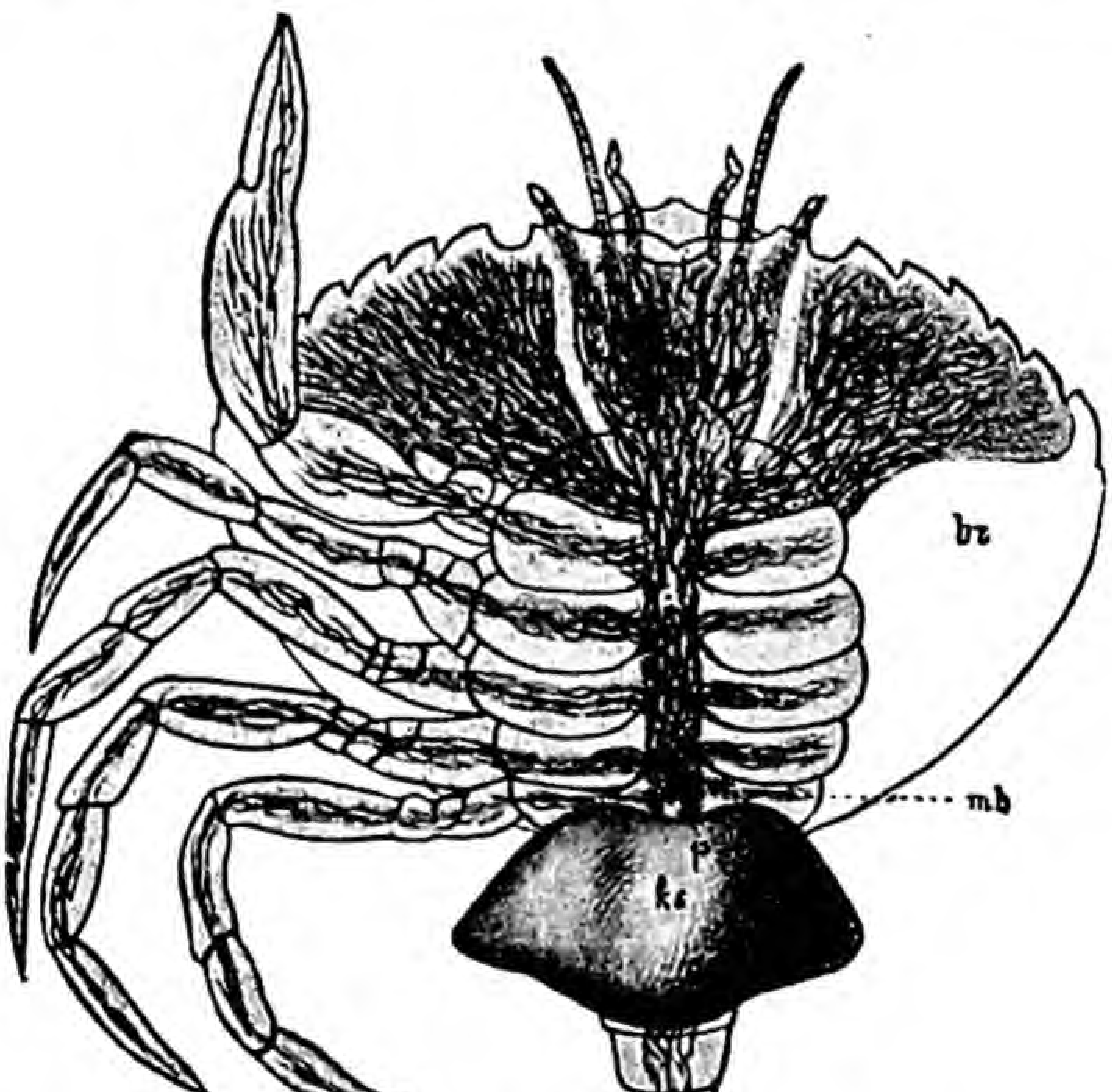


FIG. 389.—**Sacculina carcini,** on abdomen of crab. *br*. branchial region of crab; *ks*. body of parasite; *p*. peduncle; *mb*. basilar membrane, giving off root-like processes which are seen extending through the body of the host. (From Lang's *Comparative Anatomy*, after Delage.)

valvular carapace, through the opening of which the feet are protruded, and the whole animal is surrounded by a sort of parapet (*sk*) formed of six calcareous

pieces. One of these, dorsal in position, is the carina, the others appear to be represented by small calcifications developed on the peduncle of certain stalked forms such as *Pollicipes*.

Many of the *Cirripedia* are parasitic. Some of these (*Petrarca*, etc.), parasitic in Actinozoa, resemble the attached forms in essential respects; others, *e.g.*, *Alcippe*, parasitic in the shells of Molluscs Cirripedes, have abdominal but no thoracic feet. *Proteolepas*, also parasitic on other *Cirripedes*, has a maggot-like, segmented, limbless body, and a suctorial mouth.

The *Rhizocephala* are represented by *Sacculina* (Fig. 389), parasitic on Crabs, and *Peltogaster* on Hermit-Crabs. Both genera have the appearance of an immense tumour (*ks.*) on the abdomen of the host, showing no sign of segmentation, no appendages, no mouth or anus. From the attached end go off a number of delicate root-like filaments, which extend through the body of the host and absorb nutriment. Obviously degeneration is here as complete as it can well be, and nothing but the developmental history of the parasite (p. 452) would justify its inclusion among the Crustacea.

The most striking general character in the external features of the *Malacostraca* is the limitation in the number of segments. The head has the same composition as in the Entomostraca, but the thorax is invariably formed of eight segments, and, except in the Leptostraca, the abdomen of six segments and a telson. The limbs are strikingly modified for the performance of various functions.

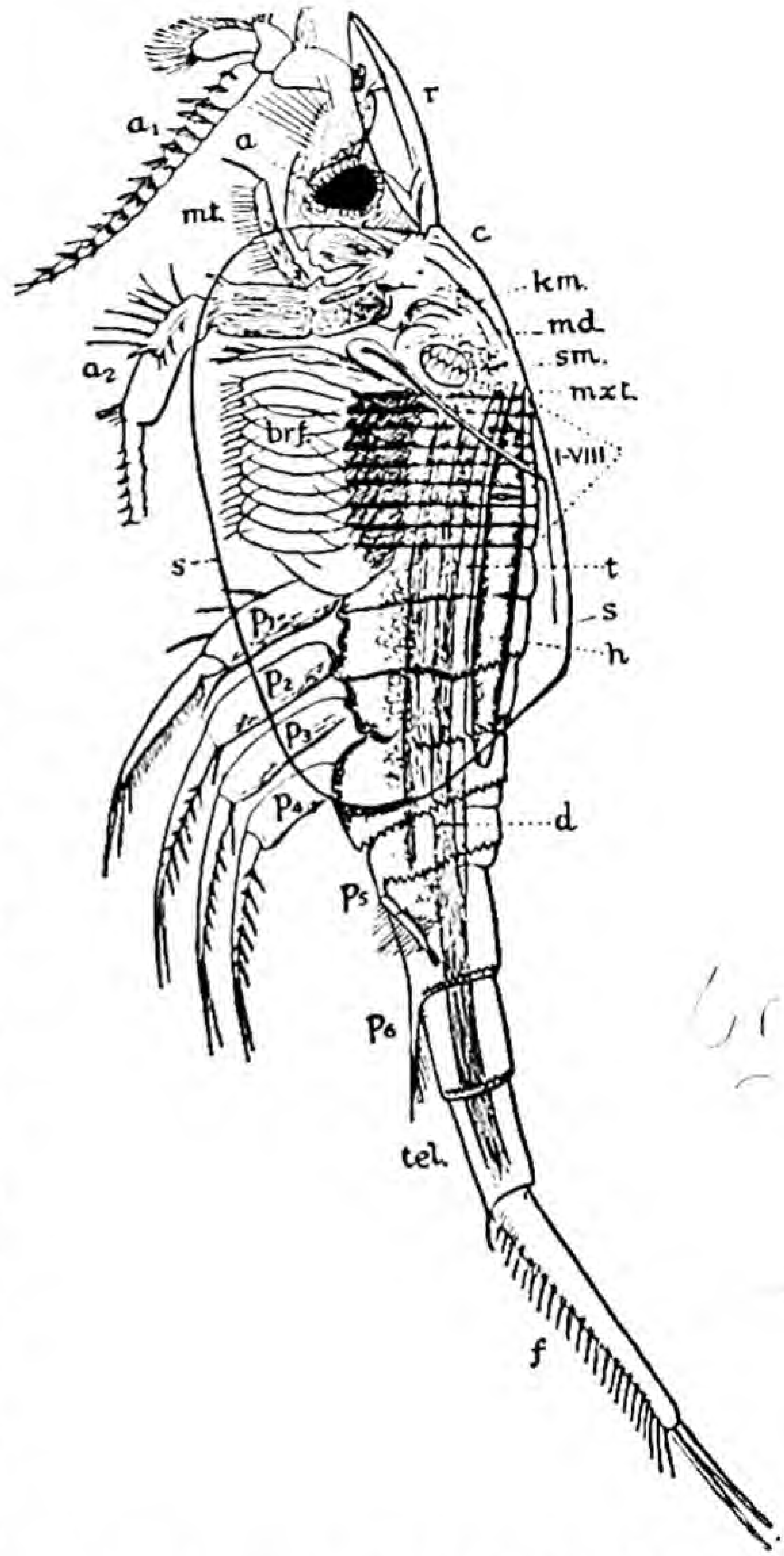


FIG. 390.—**Nebalia geoffroyi**, male. *a.* eye; a_1, antennule; a_2, antenna; *c*, head; *brf.* thoracic feet; *d*, intestine; *f.* furca; *h.* heart; *km.* gizzard; *md.* mandible; *mt.* mandibular palp; *mxt.* exopodite of second maxilla; p_1—p_4, biramous pleopods; p_5 & p_6, uniramous pleopods; *r.* rostrum; *s*, carapace; *sm.* adductor muscle; *t.* testis; *tel.* telson; *I—VIII*, thoracic segments. (From Lang's *Comparative Anatomy*, after Claus.)

The *Leptostraca* are interesting from the fact that they are annectent or linking forms between the Branchiopoda and the Copepoda on the one hand,

and the higher Crustacea on the other. The order contains only three genera, the commonest of which, *Nebalia* (Fig. 390), is a little shrimp-like marine Crustacean about 6–8 mm. in length. The body is divisible into head, thorax, and abdomen, all having the normal malacostracan number of segments except

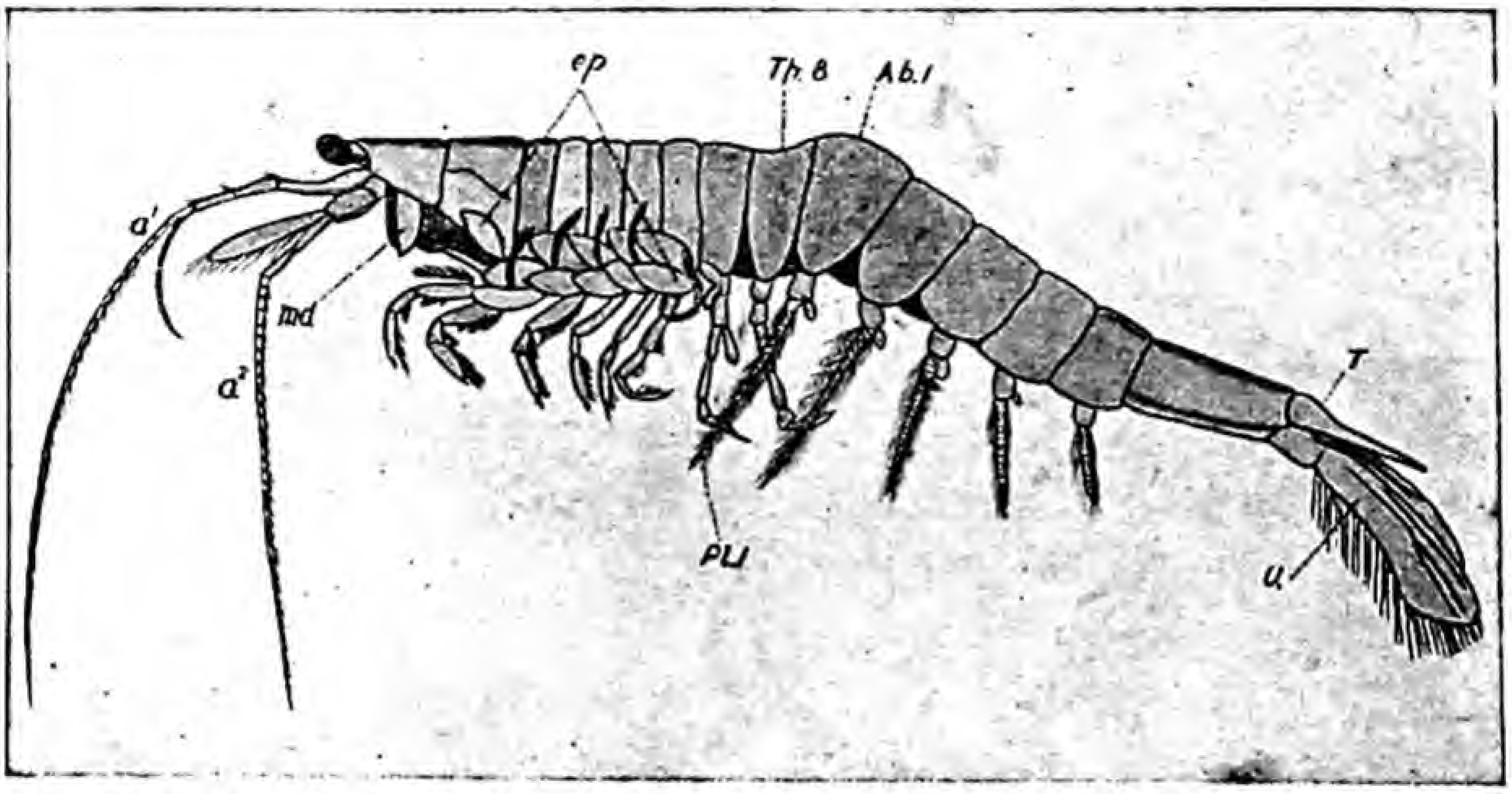


FIG. 391.—**Paranaspides lacustris,** × 4. a^1, antennules; a^2, antennæ; *Ab. 1*, first abdominal segment; *ep.* epipodites or gills on the thoracic legs; *md.* mandible; *Pl. 1*, first abdominal appendage; *T.* telson; *Th. 8*, eighth free thoracic segment; *U.* uropod. (After Geoffrey Smith.)

the abdomen, which is formed of seven segments and a telson, the latter bearing caudal styles—structures not found elsewhere in the sub-class. There is a bivalved cephalic carapace (*s.*), closed by an adductor muscle (*sm.*) and

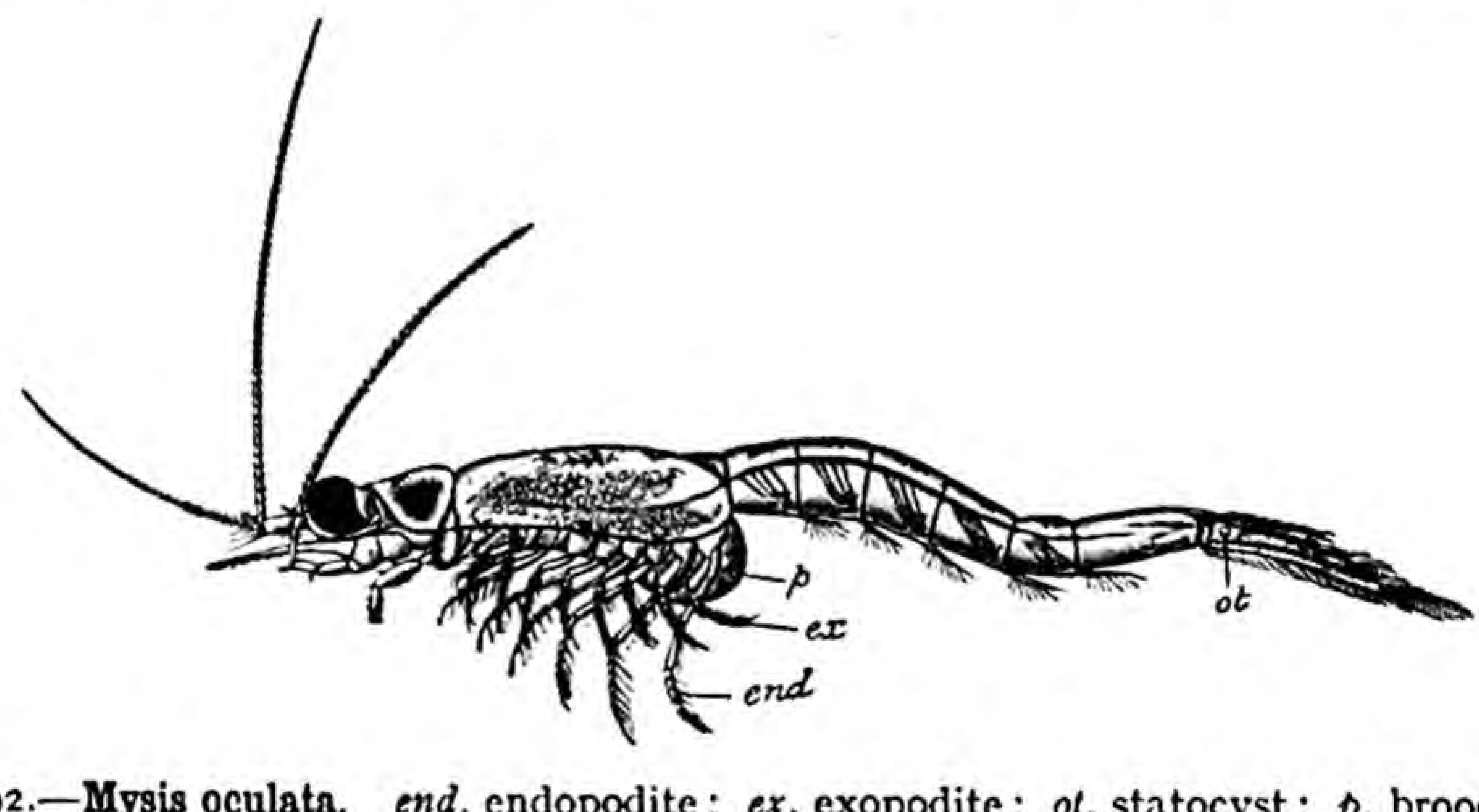


FIG. 392.—**Mysis oculata.** *end.* endopodite; *ex.* exopodite; *ot.* statocyst; *p.* brood-pouch. (After Gerstaecker.)

extending backwards to the fourth abdominal segment: it is terminated in front by a movable rostrum (*r.*).

The eyes (*a.*) are large, compound, and raised on movably articulated stalks. The antennules (a_1) and antennæ (a_2) are large, the mandibles (*md.*) have palps (*mt.*), and the exopodite of the second maxilla (*mxt.*) has the form of a slender

filament which acts as a "cleaning-foot" to keep the cavity of the carapace free from foreign bodies. There are eight thoracic appendages (*brf.*), all of them leaf-like, and recalling those of Apus. The first four abdominal appendages (p_1—p_4) are large biramous swimming-feet (pleopods), like those of Copepods; the fifth and sixth (p_5, p_6) are small and uniramous.

The Syncarida (*Anaspidacea*) (Fig. 391) are small, shrimp-like, freshwater Crustaceans, which, though resembling the rest of the Malacostraca (Eumalacostraca) in the presence of only six segments in the abdomen and the absence of caudal styles, differ from them in the possession of a combination of features which connect them more closely with certain fossil forms of Carboniferous age. Thus there is no carapace, the thoracic appendages are provided with slender respiratory exopodites, and bear a double series of epipodites or branchiæ; there are stalked eyes and a fan-like tail-fin formed of the telson and the expanded uropods.

The *Mysidacea* (Fig. 392) are small, transparent, shrimp-like forms, mostly from 2—6 mm. in length. They agree with the Crayfish in the general form of the body, in the union of the head and thorax, in the presence of a carapace—which leaves some of the posterior thoracic segments free—and in the number both of segments and appendages, but present several interesting characters indicating a lower grade of organization. One of the most notable of these is the absence of differentiation in the thoracic appendages, which, though they have a leg-like and not a leaf-like form, are all alike, none of them being modified into maxillipedes, except to a very slight degree in some forms. Moreover, the legs all possess exopodites (*ex.*), thus retaining the primitive biramous or "split-footed" form which is lost in the Decapoda. The first five pleopods are large in the male, small in the female: the sixth is a uropod, *i.e.* assists the telson in the formation of the characteristic

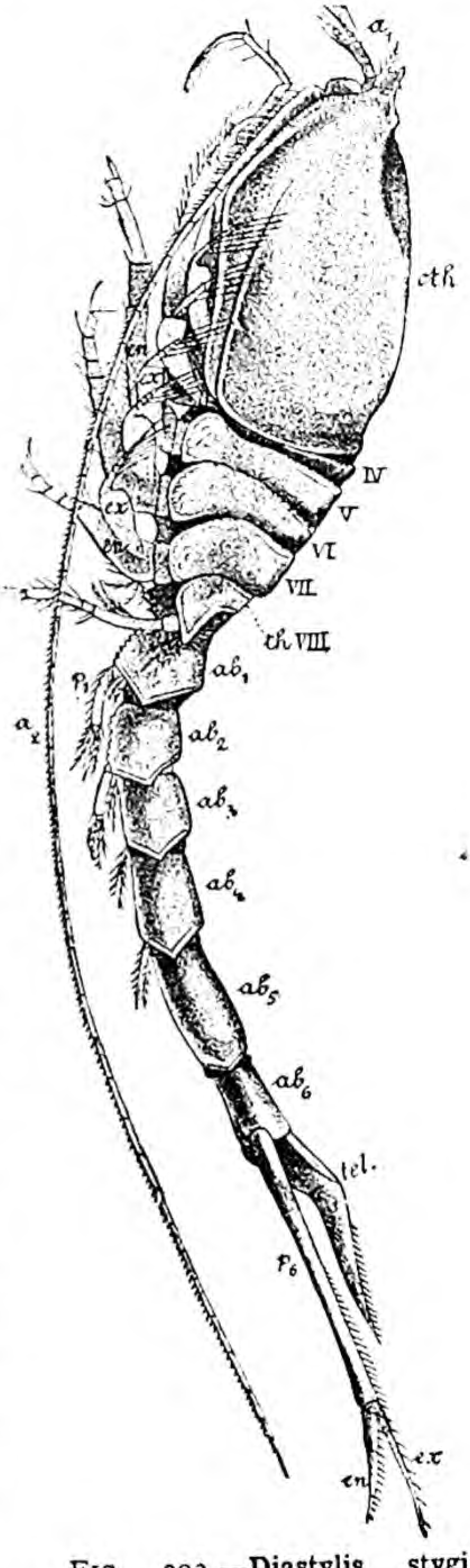


FIG. 393.—**Diastylis stygia.** a_1, antennule; a_2, antenna; ab_1—ab_6, abdominal segments; *cth.* cephalothorax; *en.* endopodite; *ex*, exopodite; p_1, p_6, pleopods; *tel.* telson; *IV–VII*, *th. VIII*, free thoracic segments. (From Lang's *Comparative Anatomy*, after Sars.)

malacostracan tail-fin: there is no trace of the entomostracan caudal styles.

The *Cumacea* are also a very small group: *Diastylis* (Fig. 393) is a good example. They are little shrimp-like animals, differing from all the Malacostraca previously considered in having poorly developed sessile eyes, sometimes fused together, and in some genera altogether absent. The carapace (*cth.*) is so small as to leave the five posterior segments (*th. IV–VIII*) uncovered. The first two pairs of thoracic limbs are maxillipedes, the last six, legs: of these two or three pairs have exopodites (*ex.*).

The *Tanaidacea*, the *Isopoda*, and the *Amphipoda*, particularly the last two

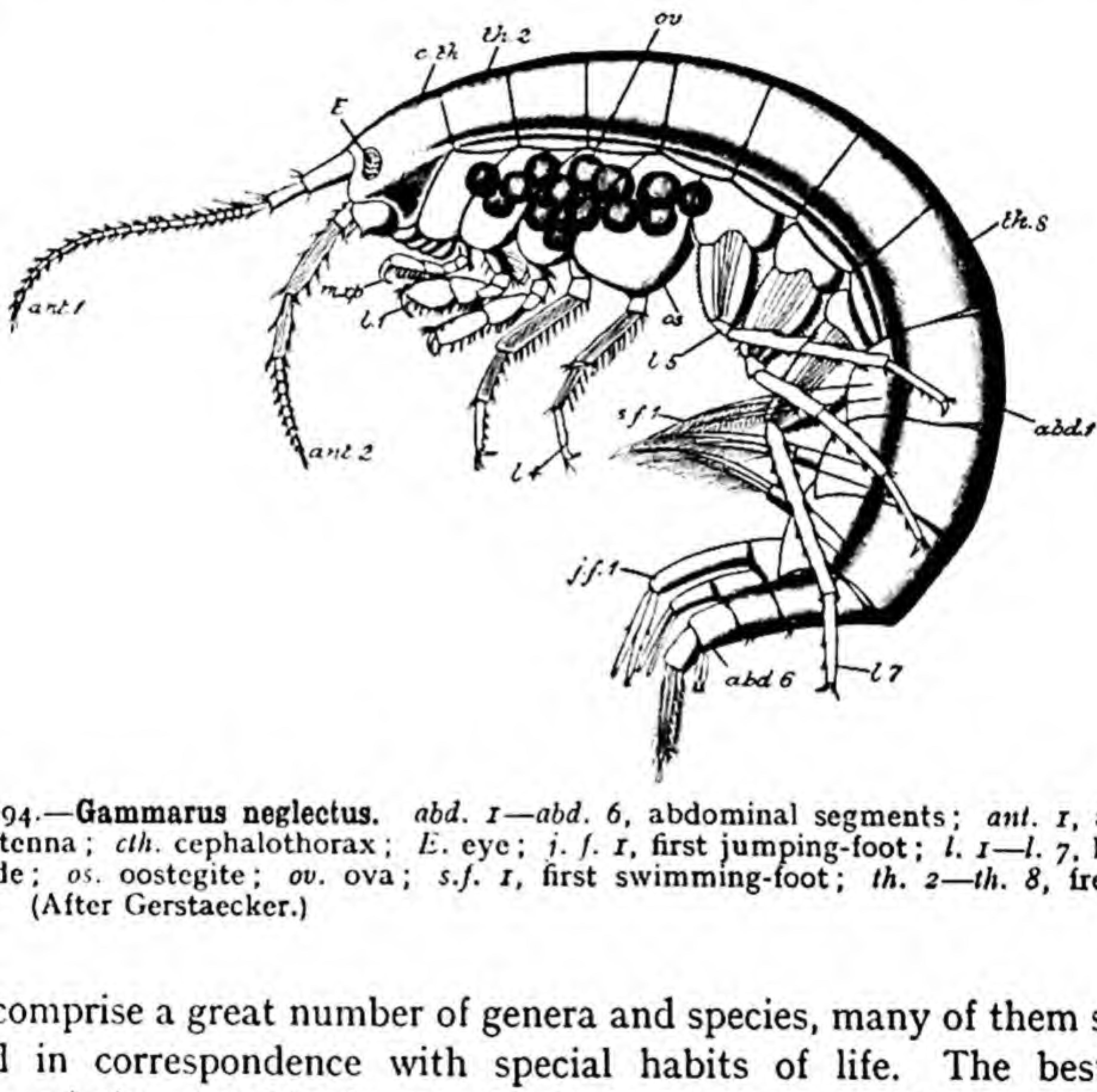


FIG. 394.—**Gammarus neglectus.** *abd. 1—abd. 6*, abdominal segments; *ant. 1*, antennule; *ant. 2*, antenna; *cth.* cephalothorax; *E.* eye; *j. f. 1*, first jumping-foot; *l. 1—l. 7*, legs; *mxp.* maxillipede; *os.* oostegite; *ov.* ova; *s.f. 1*, first swimming-foot; *th. 2—th. 8*, free thoracic segments. (After Gerstaecker.)

orders, comprise a great number of genera and species, many of them strangely modified in correspondence with special habits of life. The best known examples of the *Amphipoda* are the little Fresh-water Shrimp (*Gammarus*, Fig. 394) and the Sandhoppers (*Talitrus, Orchestia*) so common on the sea-shore. Of the *Isopoda* very convenient examples are *Asellus* (Fig. 395), common in fresh-water, and the well-known Wood-lice or Slaters (*Oniscus*, Fig. 397, 1), found under almost any piece of wood, stone, etc., which has lain undisturbed on the ground for a few weeks.

The body is usually compressed or flattened from side to side in Amphipods (Fig. 394), depressed or flattened from above downwards in Isopods (Fig. 395). The normal malacostracan number of segments is present, but the first thoracic

segment is always united with the head, so that the apparent head is really an incomplete or partial cephalothorax (*c.th.*). In the Tanaidacea (*Tanais*, etc.) the second segment of the thorax also unites with the head, and such forms form a transition to the other Malacostraca, and especially the Cumacea. In the Amphipoda and Isopoda the posterior seven thoracic segments (*th. 2–th. 8*) are free, and those of the short abdomen are usually free in Amphipods (Fig. 394, *abd. 1–6*), often more or less fused in Isopods (Fig. 395, *abd.*). In some

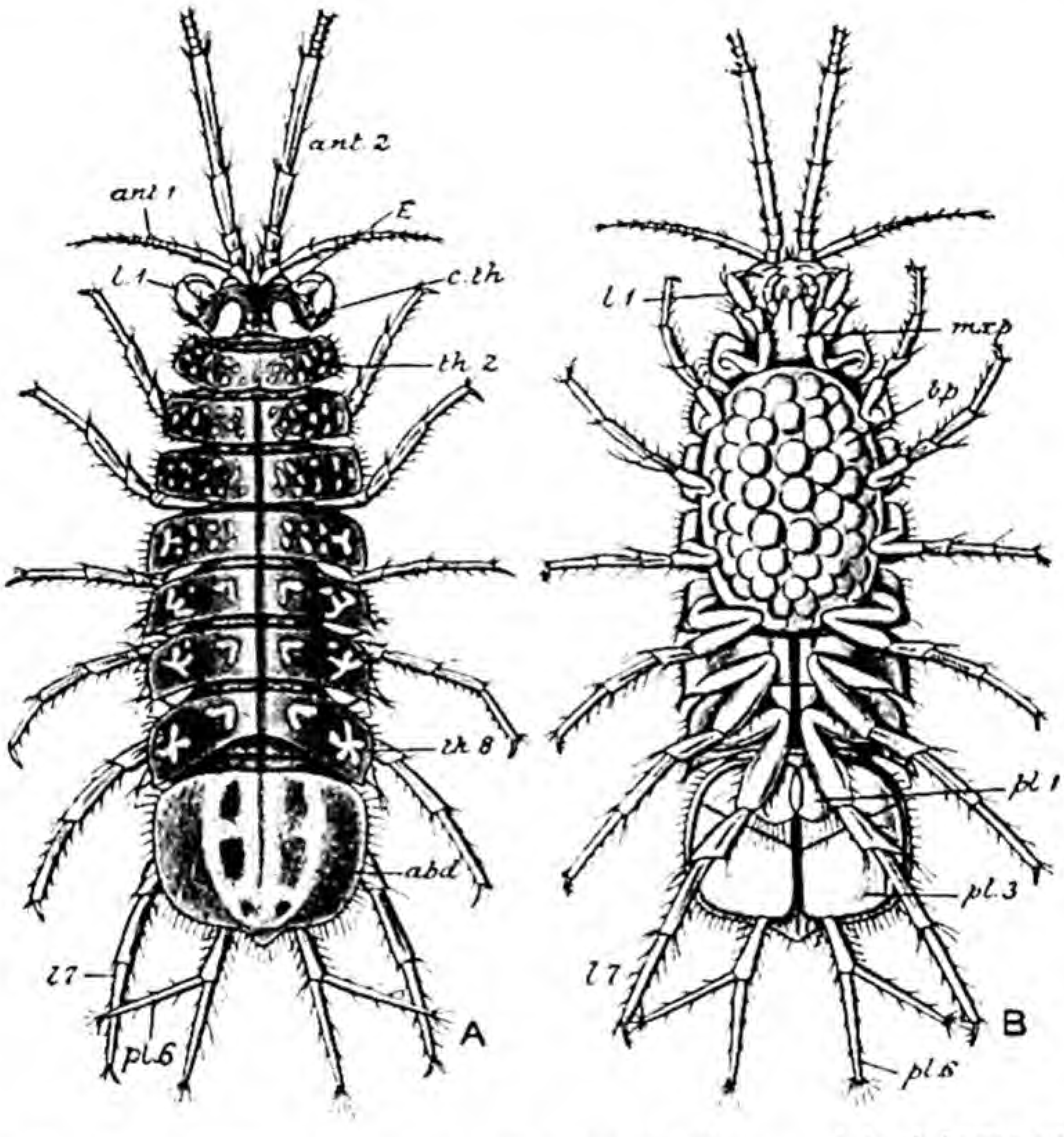


FIG. 395.—**Asellus aquaticus.** *A*, dorsal; *B*, ventral view. *abd.* abdomen; *ant. 1*, antennule; *ant. 2*, antenna; *bp.* brood-pouch; *c. th.* cephalothorax; *E.* eye; *l. 1—l. 7*, legs; *pl. 1—pl. 6*, pleopods; *th. 2—th. 8*, free thoracic segments. (After Gerstaecker.)

Isopoda the thoracic segments are produced laterally into large and prominent pleura.

The eyes (*E*) are compound and usually sessile: they are, however, stalked in some of the less specialized members of the order, a circumstance which lends support to the view that the sessile eyes have, in this particular group, arisen by the atrophy of eye-stalks. The antennæ (*ant. 2*) as well as the antennules (*ant. 1*) are uniramous, or the former bear a minute exopodite. The first pair of thoracic appendages (*mxp.*) are modified to form maxillipedes, which are sometimes united together in the middle line so as to form a sort of lower lip. The remaining seven thoracic appendages take the form of legs (*l. 1–l. 7*) which

are usually arranged in two groups, four of them directed forwards and three backwards, or *vice versa*. The legs end either in simple claws or in large subchelæ (p. 446): vestigial expodites are present in some Tanaidacea. In the female, certain of the legs bear flat plates, the *oostegites* (Fig. 394, *os*), probably modified epipodites, which enclose a brood-pouch for the reception of the eggs. In Amphipods the gills are also borne on the legs.

The abdominal appendages are very different in the two orders. In Amphipoda the first three are biramous swimming-feet (Fig. 394, *s. f.*), the last three peculiar stiff processes used for jumping (*j. f.*). In Isopods more or fewer of the pleopods have broad plate-like endo- and exo-podites (Fig. 395, *pl. 3*), the

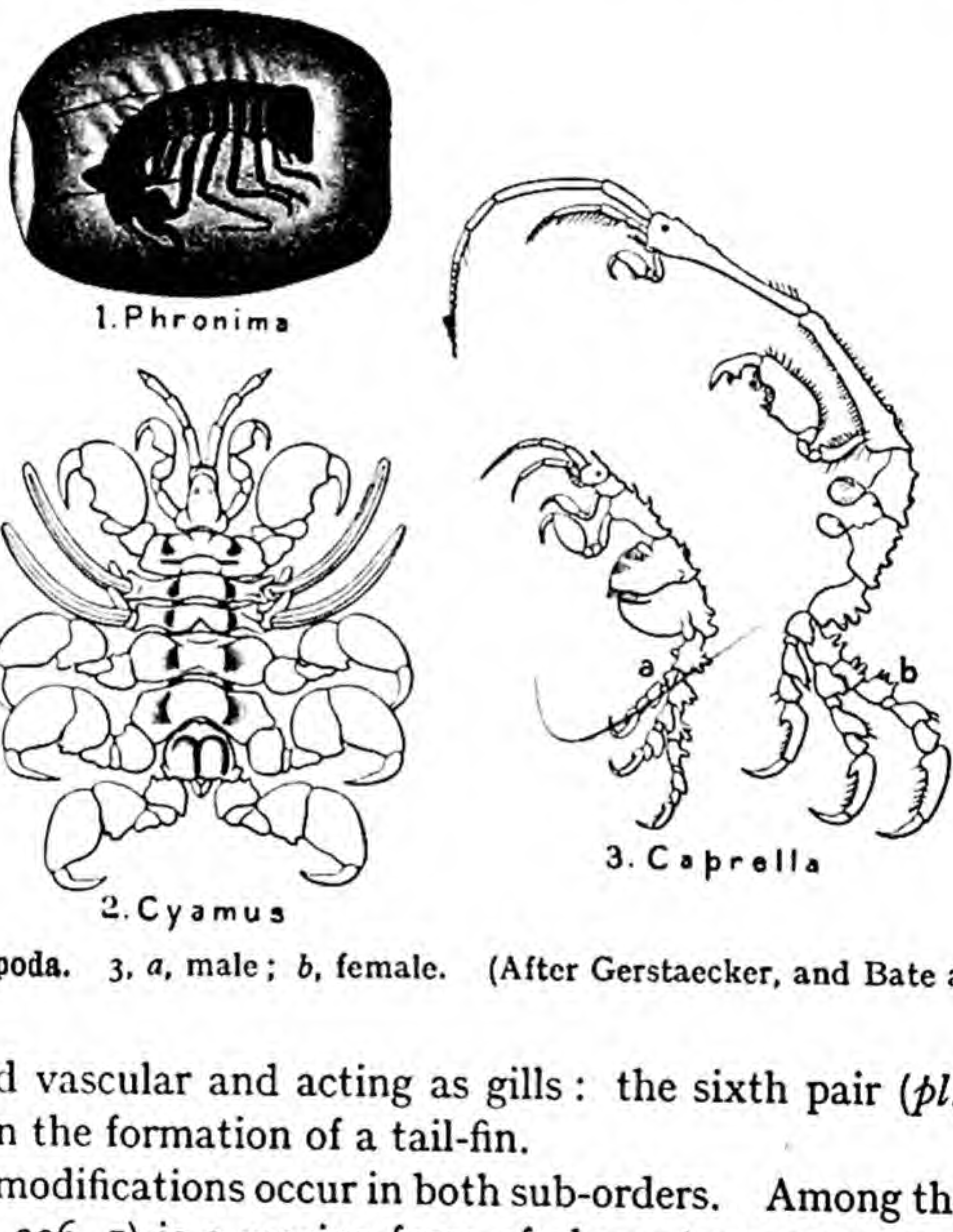


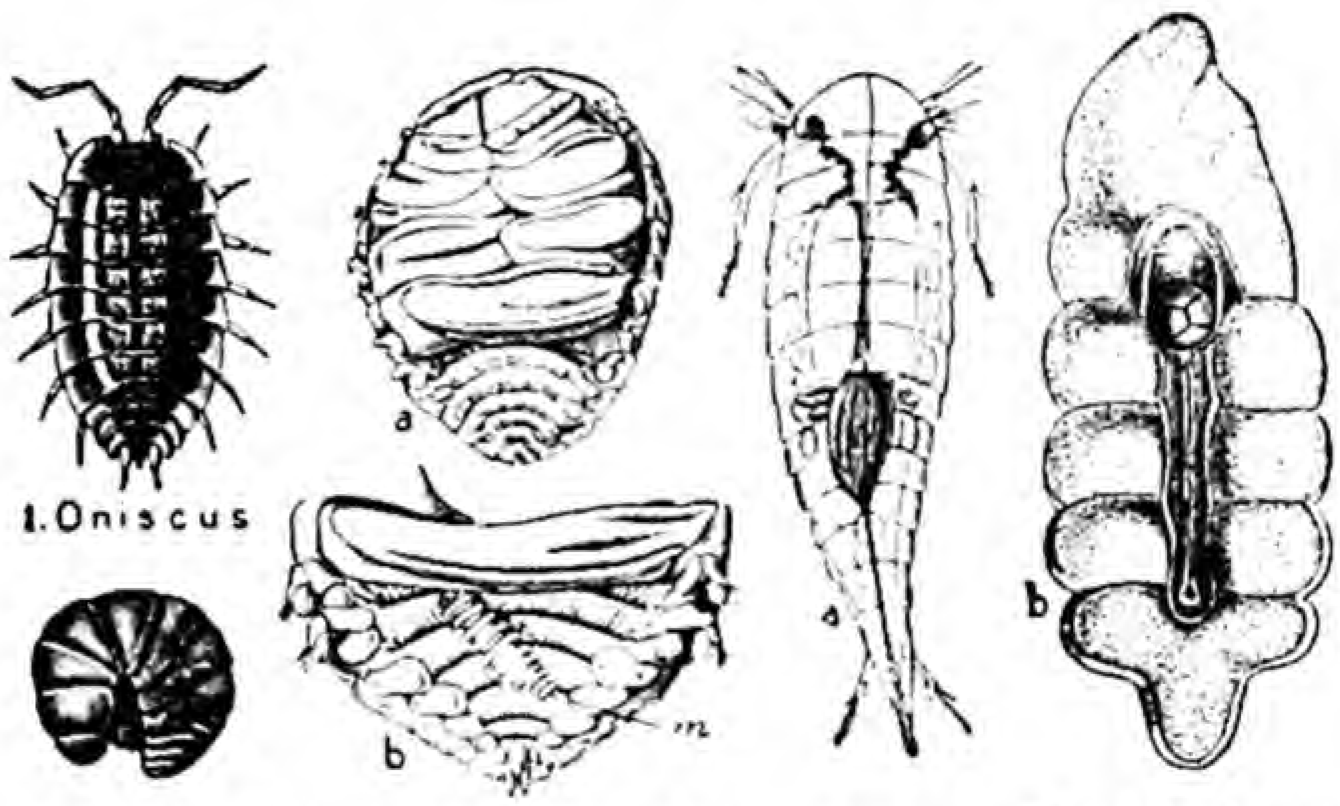
FIG. 396.—**Amphipoda.** 3, *a*, male; *b*, female. (After Gerstaecker, and Bate and Westwood.)

former thin and vascular and acting as gills: the sixth pair (*pl. 6*) are either leg-like or aid in the formation of a tail-fin.

Interesting modifications occur in both sub-orders. Among the Amphipoda, *Phronima* (Fig. 396, 1) is a marine form of glassy transparency, the female of which inhabits a transparent barrel-like structure—the test of a pelagic Tunicate—in which she brings up her young. *Caprella* (3) is a singular creature in which the abdomen is quite vestigial, and the rest of the body, as well as the appendages, extremely slender. It creeps about on colonies of Hydrozoa and Polyzoa, to the branches of which its own form and colour are so closely assimilated as to render it difficult of detection. The allied *Cyamus* (Whale louse) (2) is parasitic on the skin of whales: it also has a vestigial abdomen, but

the body—exceptionally among Amphipods—is broad and depressed, and the legs are curiously swollen.

Among the Isopoda, one of the most interesting forms is the common Wood-louse (Fig. 397, 1), which is almost unique among Crustacea for its perfect adaptation to terrestrial life. The allied "Pill-bugs" (*Armadillidium*, 2) have the habit of rolling themselves up into a ball when disturbed. *Cymothoa* and its allies are large species (6–8 cm. in length) parasitic in the mouths of Fishes, where they hold on to the mucous membrane with their short, clawed legs: their mouth-parts are often modified for sucking. In the *Bopyrini*, found in the gill-cavities of various Crustacea, parasitism is accompanied by great degeneration and asymmetry, as well as by a notable degree of sexual dimorphism, the males (3 *b*, *m*) being very small and permanently attached to the



2. Armadillidium. 3. Gyge. 4. Cryptoniscus.

FIG. 397.—**Isopoda.** 3, *a*, entire animal; *b*, posterior end with attached male (*m*); 4, *a*, larva; *b*, adult female. (After Cuvier, Claus, and Gerstaecker.)

bodies of the females. Lastly, in *Cryptoniscus*, parasitic on Rhizocephala, the adult female (4 *b*) has no trace of crustacean organization, and it is only by the study of development that its true systematic position can be guessed.

In the division Eucarida, the *Euphausiacea* (Fig. 405) are pelagic forms in which none of the thoracic appendages are modified so as to take the form of maxillipedes, and in which there is only a single series of branchiæ (podobranchs).

Amongst the *Decapoda* are included nearly all the largest and most familiar Crustacea—the Prawns and Shrimps, Lobsters, Crayfishes, and Crabs. The cephalothorax is always completely covered by the carapace. The three anterior pairs of thoracic appendages are modified into maxillipedes, which retain the original biramous character, but the five posterior pairs are enlarged, and form legs, which are always—except as an individual variation—devoid of exopodites in the adult.

In the Shrimps and Prawns (Fig. 398) the body is compressed, and the exoskeleton is not calcified. The abdomen is very large in proportion to the cephalothorax, and has a peculiar bend close to its junction with the thorax. The legs are very slender, are used for swimming, not walking, and sometimes

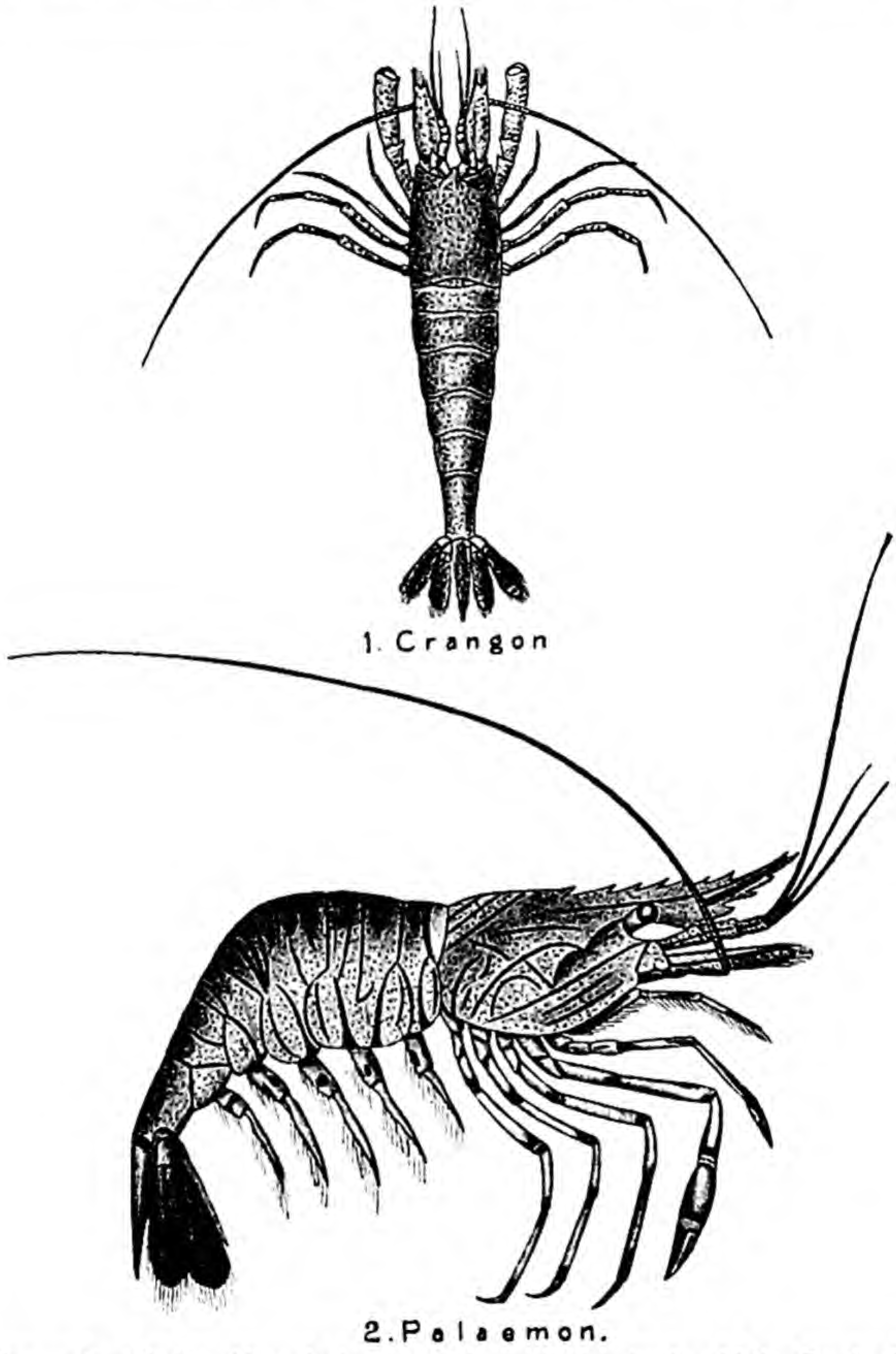


FIG. 398.—**Shrimp** (dorsal view) and **Prawn** (side view). (After Cuvier.)

one pair, sometimes another, is enlarged to form the chelipeds. The rostrum is large—sometimes longer than the rest of the carapace—and the eye-stalks, antennæ, and legs may attain extraordinary dimensions.

The Lobsters and fresh-water Crayfishes agree with Astacus in all essential

details, but the sea-Crayfishes (*Palinurus*) present some striking modifications. There are no chelæ, the legs all ending in simple claws: the antennæ are of immense size, and their proximal segments are fused with one another and with the carapace, quite crowding out the epistoma: the rostrum is reduced, or even vestigial, and the pleopods are very broad and fin-like. In *Scyllarus* (Fig. 399) and its allies the body is broad and depressed, the bases of the legs widely separated from one another by the broad sterna, the antennæ (*ant.* 2) short and plate-like, and the eye-stalks (*E*) enclosed in socket-like grooves of the carapace. Most of these characters show an approximation to what is found in the Crabs.

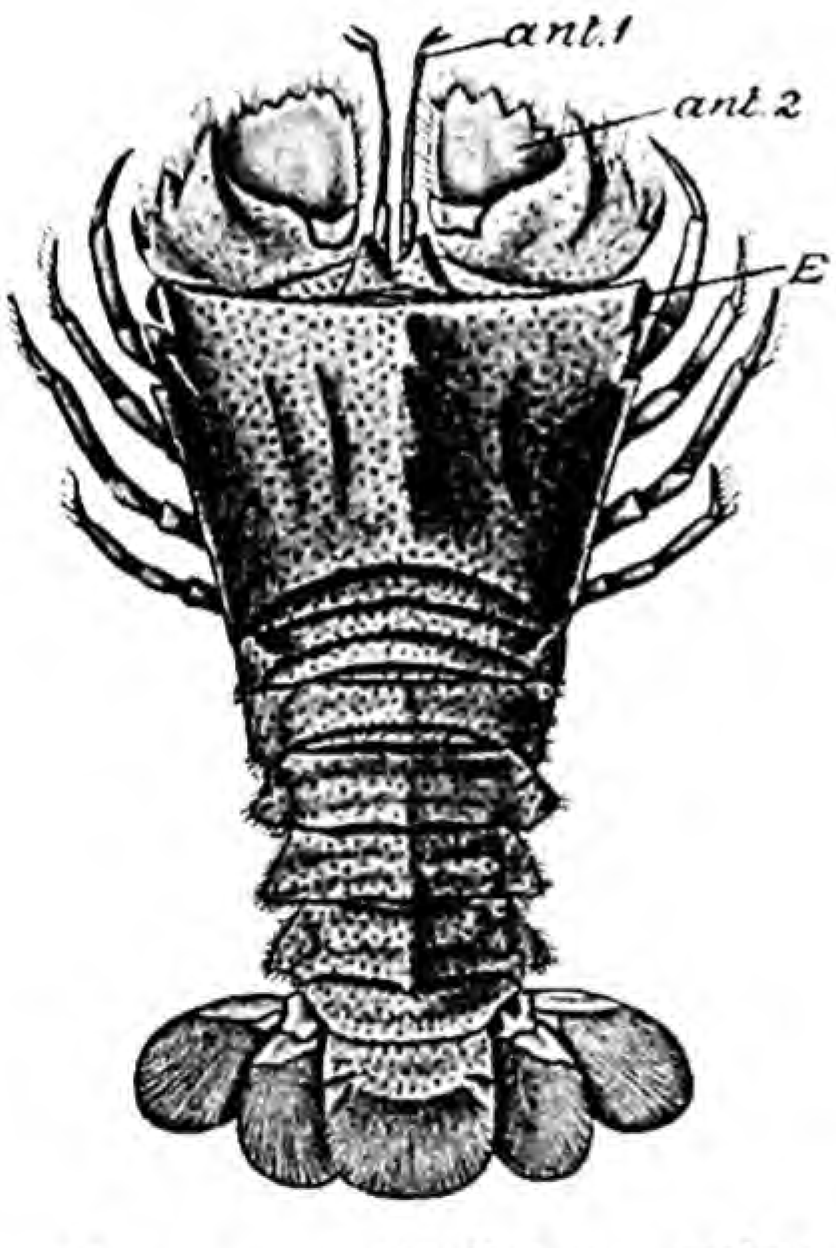


FIG. 399.—**Scyllarus arctus.** *ant.* 1, antennule; *ant.* 2, antenna; *E.* eye. (After Cuvier.)

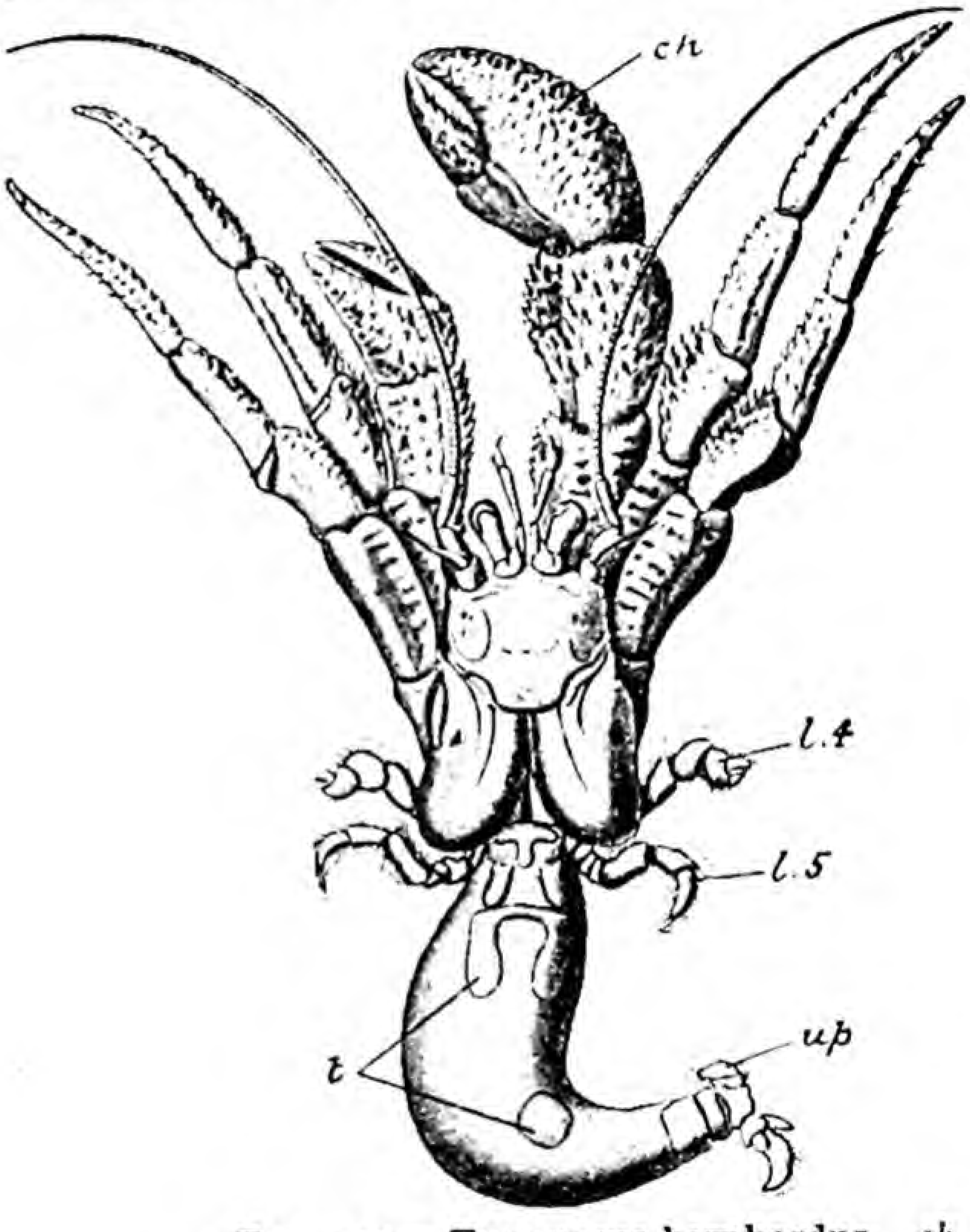


FIG. 400.—**Eupagurus bernhardus.** *ch.* chela of first right leg; *l.* 4, *l.* 5, fourth and fifth legs; *t.* abdominal terga; *up.* uropods. (After Bell.)

Of the *Anomura*, the Hermit-Crabs (*Eupagurus*, etc., Fig. 400) are very strangely modified in relation with their peculiar mode of life. They are always found inhabiting the empty shells of Gastropods (Whelks, Periwinkles, etc.), the abdomen, which has become spirally twisted, completely enclosed within the shell and only the cephalothorax protruding. In correspondence with this mode of protection, the abdomen is soft, having only vestiges of terga (*t.*) on the dorsal side, and its appendages are more or less atrophied except the sixth pair (*up*), which take the form of a pair of hooks, and are used to hold on to the columella of the shell. The fifth pair of legs (*l.* 5) are much reduced, and in some

species one of the chelipeds is greatly enlarged and its chela (*ch.*) acts as an operculum, completely closing the mouth of the shell when the animal is retracted, or both chelipeds are enlarged to perform this function. As the Hermit-Crab grows it takes up its abode in larger and larger shells, sometimes killing and removing piecemeal the original inhabitant.

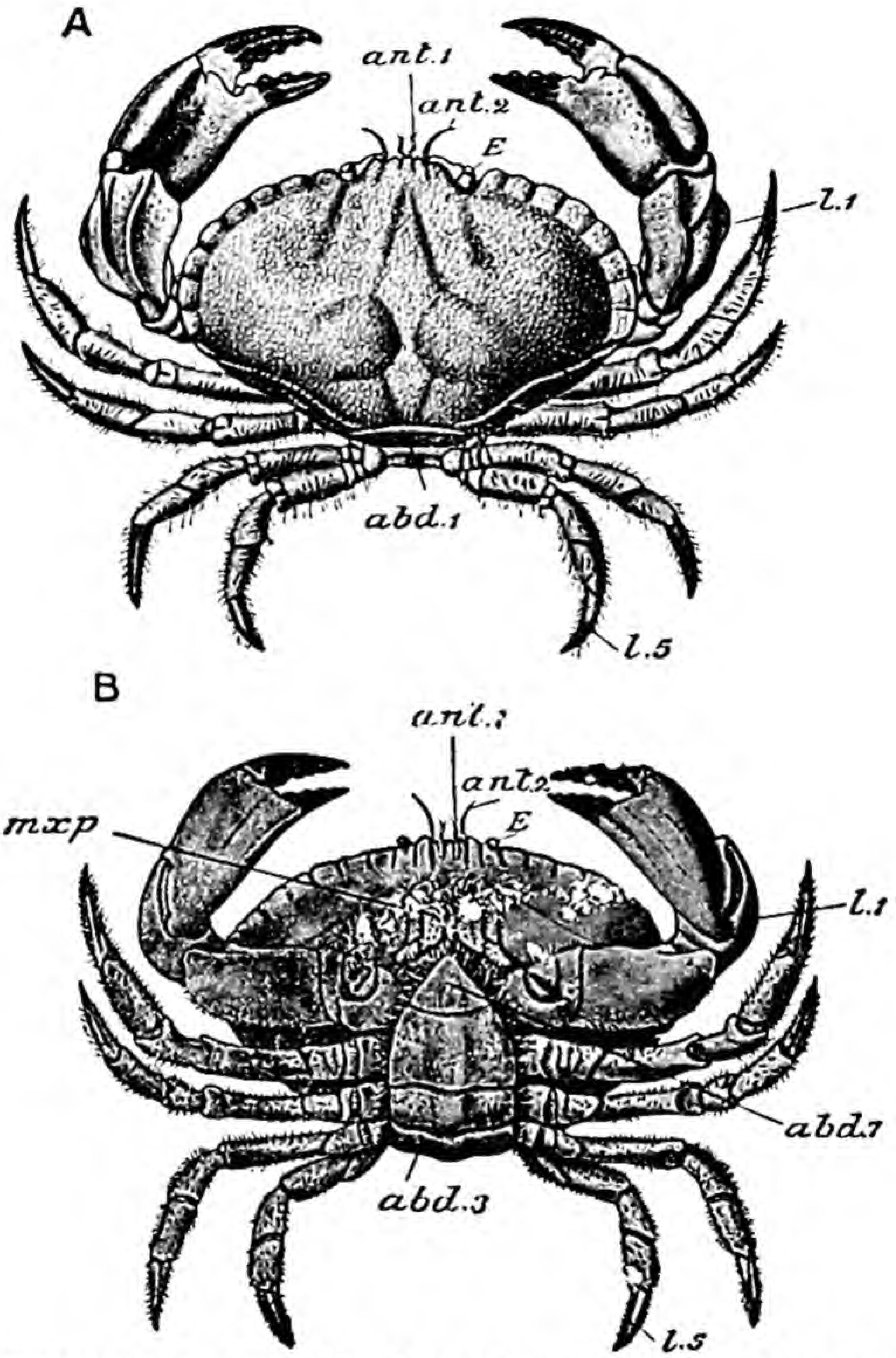


FIG. 401.—**Cancer pagurus.** *A*, dorsal; *B*, ventral aspect. *ant. 1*, antennule; *ant. 2*, antenna; *abd. 1*, *abd. 3*, *abd. 7*, abdominal segments; *E.* eye-stalk; *l. 1*, *l. 5*, legs; *mxp. 3*, third maxillipedes. (After Bell.)

Other Anomura, such as the Cocoa-nut Crab (*Birgus*), *Hippa*, etc., approach the Brachyura in the short, more or less permanently flexed abdomen, but are clearly separated from them by the structure of the head and its appendages.

In the *Brachyura*, or true Crabs, we reach the highest degree of specialization known among the Crustacea. The cephalothorax (Fig. 401) is always of great

proportional breadth, and is frequently much broader than long. The abdomen, on the other hand, is greatly reduced, its sternal region is uncalcified, and it lies permanently flexed in a groove on the very broad thoracic sterna, so

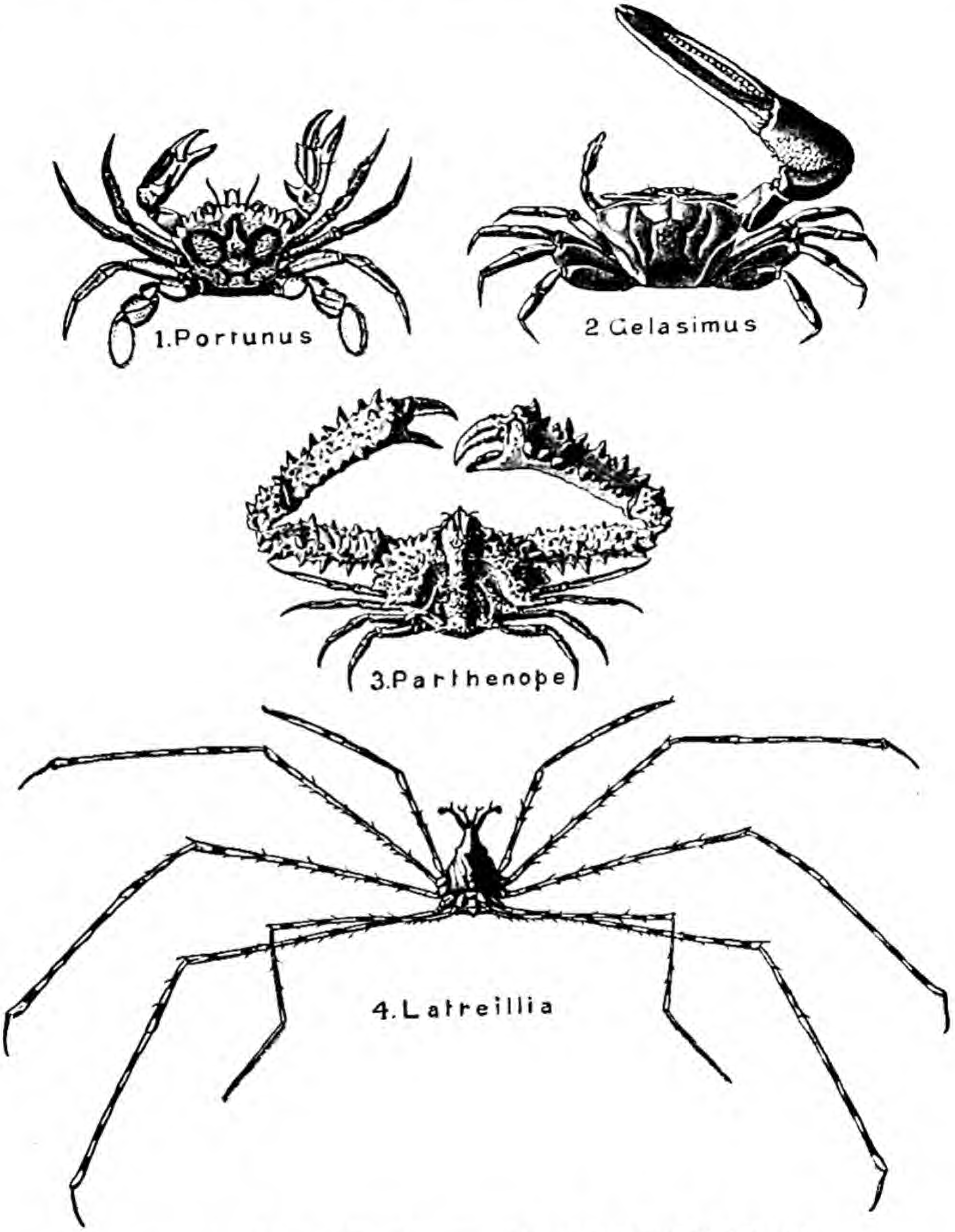


FIG. 402.—Typical **Brachyura.** (After Bell and de Haan.)

as to be often quite hidden in a view from above. In correspondence with this the pleopods are much reduced, the male retaining only two pairs as copulatory organs, the female four pairs for the attachment of the eggs. The uropods are absent, so that there is no tail-fin. The eye-stalks (E) are contained in *orbits*

or sockets of the carapace, which are so prolonged that the eyes appear to arise behind the antennules and antennæ. Both pairs of feelers are small, and the bases of the antennules are contained in sockets or *fossettes*. The third maxillipedes (*mxp.*) are broad, flat, and valve-like, not leg-like as in the Macrura. The first legs (*l.1*) form chelipeds often of great size: the remaining legs generally end in simple claws, but in the Swimming-crabs (Fig. 402, 1) the distal segment in the fifth pair is flattened and forms a fin. The range of variation in form, proportions, colour, markings, etc., among Crabs is very great (Fig. 402).

Unlike the Decapoda, the *Stomatopoda* form a very small order, comprising a few genera varying from the size of a Shrimp to that of a Lobster. *Squilla* (Fig. 403) is the best known genus.

The abdomen is very large in proportion to the cephalothorax, and the carapace (*cth.*), which is thin and uncalcified, leaves the last three thoracic

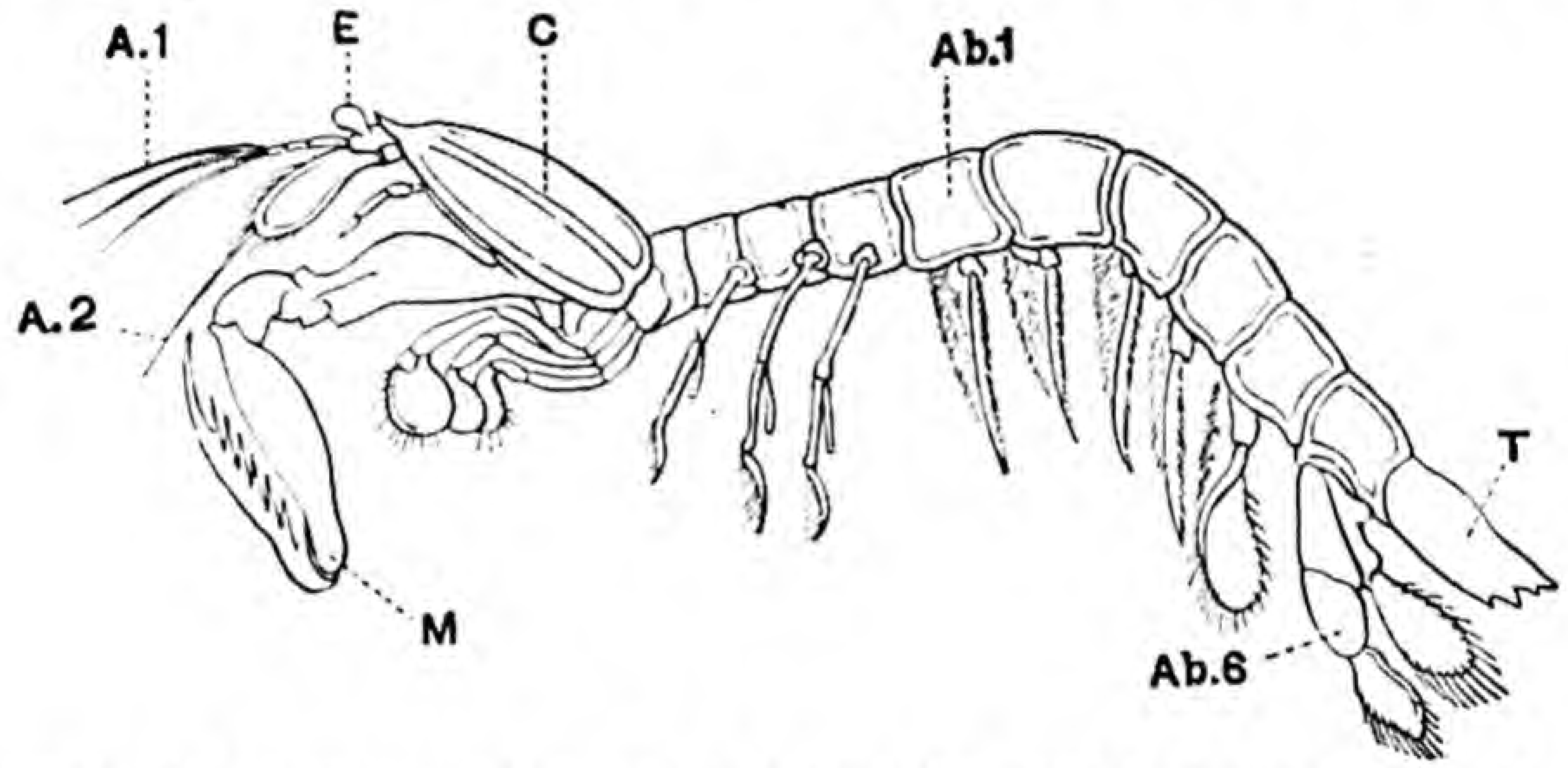


FIG. 403.—**Squilla sp.**, lateral view. *A. 1*, antennule; *A. 2*, antenna; *Ab. 1*, first abdominal segment; *Ab. 6*, sixth abdominal appendage; *C.* cephalothorax; consisting of the head fused with the first five thoracic segments; *E.* eye; *M.* second maxilliped; *T.* telson. (From the *Cambridge Natural History*, Macmillan & Co., Ltd., after Gerstaecker and Ortmann.)

segments uncovered. The rostrum is movably articulated, and covers the anterior head-region, which is divided into two distinct segments, the first bearing the large stalked eyes, the second the antennules. This division is absent in the larva, and does not appear till the proper segmentation of the body is established: probably it has a physiological meaning, and is connected with the necessity of extreme mobility of the eyes and olfactory organs in an animal which lives in a burrow with only the anterior end of the head exposed.

The antennule (*A. 1*) has three flagella; the antenna (*A. 2*) a single flagellum and a very large exopodite. The first five pairs of thoracic limbs (*1—5*) are turned forwards towards the mouth, and act as maxillipeds; the second of these—corresponding with the second maxilliped of Astacus—is very large (*M*), and its distal segment is turned back and articulated to the penultimate segment like the blade of a pocket-knife to the handle. In this way a very efficient weapon called a *sub-chela* is produced, both the segments of which are

produced into strong spines. The remaining three thoracic appendages are slender legs provided with exopodites: the last of them has a styliform copulatory organ developed from its proximal segment. The pleopods are large and biramous: the first five have gill-filaments attached to their plate-like exopdites: the sixth (Ab. 6) form large uropods or lateral tail-lobes, as in Astacus.

With regard to the **texture of the exoskeleton**, there is every graduation from the delicate polished cuticle of most Branchiopoda, Ostracoda, Copepoda, etc., through the calcified but still flexible cuticle of Astacus, to the thick, tuberculated, stony armour of many Crabs (Fig. 402, 3), or the shelly pieces of Cirripedes. The exoskeleton is secreted from a single-layered ectoderm, and undergoes periodical moults or ecdyses. There is no transverse layer of **muscle,** and the longitudinal layer is broken up into paired dorsal and ventral bands. As a rule, each limb-segment is acted upon by two muscles: the joints are nearly always hinge-joints.

The **body-cavity** consists of several chambers separated from one another by partitions. In *Palæmonetes*, one of the Prawns, there is a median dorsal chamber enclosing the ophthalmic artery, and not containing blood: it is probably a portion of the cœlome in the strict sense of the word. The cavities of the gonads are also cœlomic, and the ducts by which they communicate with the exterior are probably modified cœlomoducts. In addition to these cavities there is a large central space, in which the enteric canal, digestive glands, gonads, etc., lie; paired lateral spaces containing portions of the shell-gland; spaces in the limbs; and the pericardial sinus, in which the heart lies. All these cavities contain blood, and constitute a body-cavity, formed by the enlargements of blood-vessels, which have largely replaced the true cœlome. Such a blood-containing body-cavity is called a *hæmocœle*.

The **enteric canal** consists of a vertical gullet, an expanded "stomach," and a nearly straight horizontal intestine. In some of the Cladocera the intestine is coiled, but this is quite exceptional. In the lower Crustacea, part or the whole of the "stomach" is formed from the mesenteron, but in Malacostraca both gullet and "stomach" (gizzard) are developed from the stomodæum. A "gastric mill" is present in Malacostraca, and a rudiment of such an apparatus occurs in Ostracoda. The digestive glands are usually branched cæca formed as offshoots of the mesenteron: in the Isopoda and Amphipoda (Fig. 404, *l*) they are unbranched cæca extending into the abdomen: in Stomatopoda they consist of ten metamerically arranged organs opening into the intestine. In Amphipods there is an unpaired intestinal cæcum (*ud.*) or a pair of cæca which may have an excretory function (*hd.*). So-called salivary glands, opening on the labrum, have been found in several genera.

In most of the Branchiopoda, Ostracoda, Copepoda, and Cirripedia, respiration takes place by the general surface of the body, and the only **respiratory organs** are specially modified parts of the appendages. In the stalked Barnacles,

however, there are delicate processes attached to the feet, which are supposed to be rudimentary gills. Amongst the Malacostraca also, the Leptostraca, many Mysidacea, and the Cumacea have no specialized respiratory organs, but the

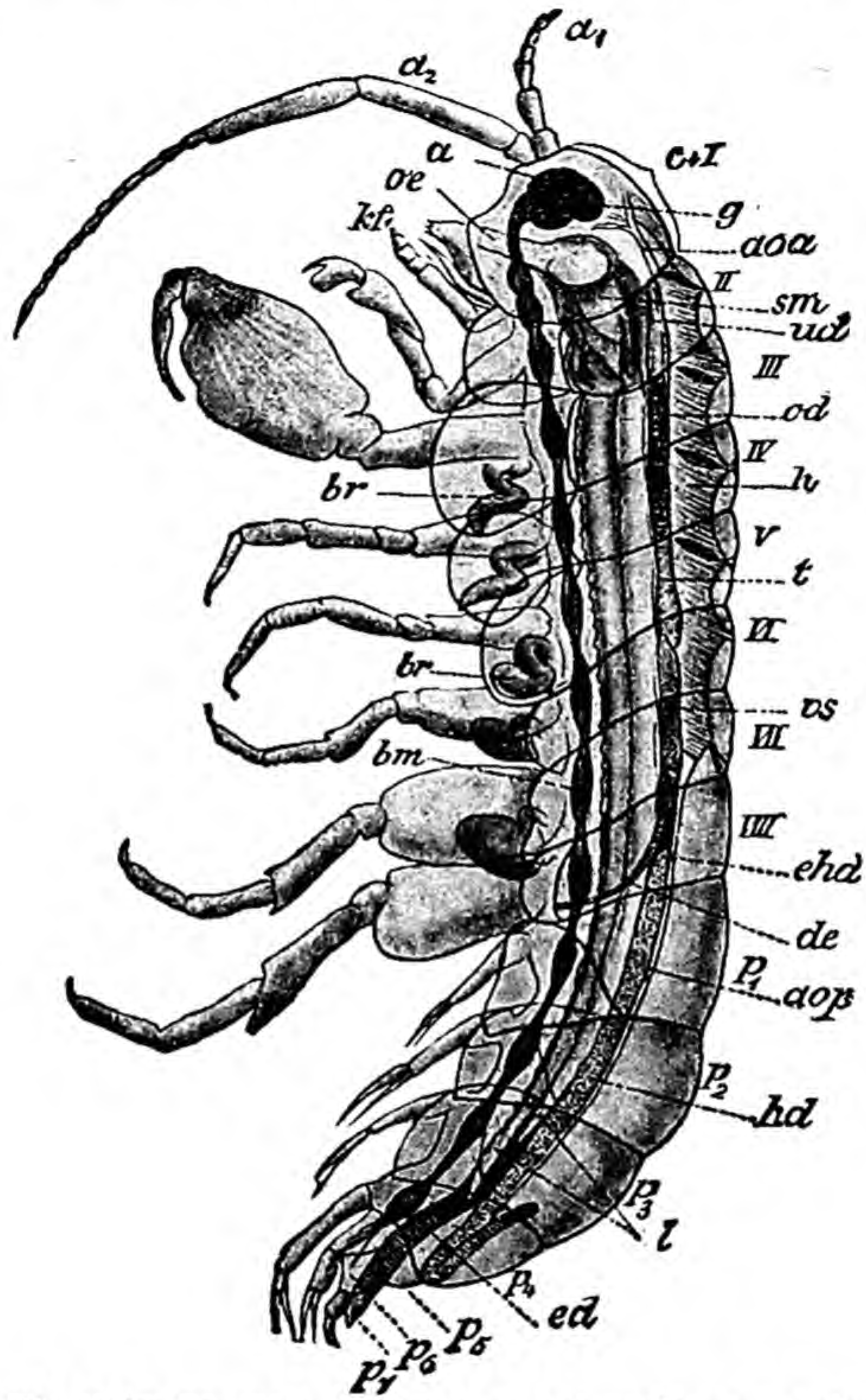


FIG. 404.—**Orchestia cavimana,** male. *a.* eye; a_1, antennule; a_2, antenna; *aoa*, anterior aorta; *aop*, posterior aorta; *bm*, ventral nerve-cord; *br*, gills; *C + T*, cephalothorax; *de*, vas deferens; *ed*, rectum; *ehd*, entrance of excretory cæcum into intestine; *g*, brain; *h*, heart; *hd*, excretory cæcum; *kf*, maxilliped; *l*, digestive glands; *od*, anterior part of gonad in which small ova are often found in young males; *oe*, gullet; p_1—p_7, abdominal segments; *sm*, "stomach"; *ud*, intestinal cæcum; *vs.* vesicula seminals; *t*, testis; *II–VIII*, free thoracic segments. (From Lang's *Comparative Anatomy*, after Nebesky.)

Euphausiacea possess tufted podobranchiæ (Fig. 405) quite uncovered by the carapace. In the Decapoda the gills may be either plume-like, as in Astacus and its allies, or the soft cylindrical gill-filaments may be replaced by flat plates, as in Crabs and many Prawns. It is in this order only that we find

the three types of gill described in Astacus, and the examination of numerous forms leads to the conclusion that the typical or theoretical branchial formula for the group is as shown in the table below.

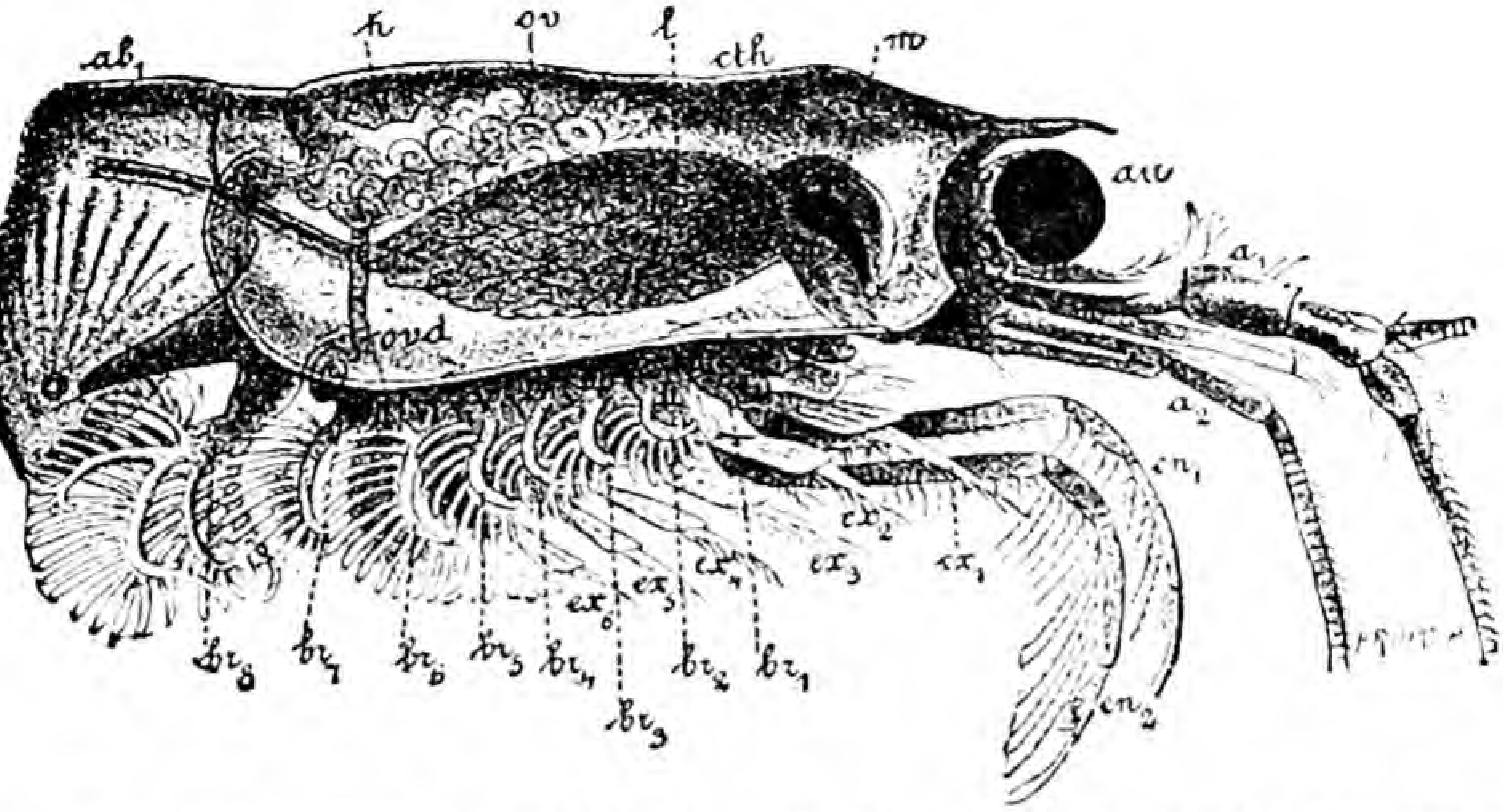


FIG. 405.—Anterior portion of **Euphausia pellucida.** $a._1$, antennule; $a._2$, antenna; $ab._1$, first abdominal segment; *au*, eye; $br._1$—$br._8$, podobranchiæ; *cth.* cephalothorax; $en._1$, $en._2$, endopodites of first two thoracic limbs; $ex._1$—$ex._6$, exopodites of first six thoracic limbs; *h*, heart; *l*. digestive gland; *m*. "stomach"; *ov*. ovary; *ovd*. oviduct; *I—VIII*, protopodites of thoracic limbs. (From Lang's *Comparative Anatomy*.)

Actually, however, this formula never occurs, as there is always more or less reduction in the number of gills. Palinurus has the highest number known, viz., twenty-one, and in the Common Crab the total number is only nine.

THORACIC SEGMENTS.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	TOTAL.
Podobranchiæ .	1+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	1+*ep*	8+8*ep*
Arthrobranchiæ	2	2	2	2	2	2	2	2	16
Pleurobranchiæ	1	1	1	1	1	1	1	1	8
TOTAL .	4+*ep*	4+*ep*	4+*ep*	4+*ep*	4+*ep*	4+*ep*	4+*ep*	4+*ep*	32+8*ep*

Many Crabs live on land, and the gills are enabled to discharge their function in virtue of the moisture retained in the nearly closed gill-chamber. In the Cocoa-nut Crab (*Birgus*) the upper part of the gill-chamber is separated from the rest and forms an almost closed cavity into which vascular tufts project: it thus functions as a true lung.

In Amphipoda, also, the gills (Fig. 404, *br.*) are outgrowths of the thoracic limbs: in Isopods they are the modified endopodites of the second to the fifth pleopods; in some of the terrestrial forms, in adaptation to aërial respiration, a system of air-tubes is developed in the exopodites; in Stomatopoda, gill-

filaments spring from the exopodites of the first to the fifth pleopods. Moreover many Crustacea perform rhythmical contractions of the intestine, taking in and expelling water: such *anal respiration* is common among the lower groups, and is especially noticeable in Cyclops.

The **heart** is absent in many Copepods (including Cyclops), in some Ostracoda (including Cypris), and in Cirripedia: it is an elongated tube with several pairs of ostia in the first three orders of the Branchiopoda, in the Leptostraca, Stomatopoda, Anaspidacea, Tanaidacea, Isopoda, and Amphipoda (Fig. 404, *h.*); in Cladocera and Decapoda it is shortened to an avoid sac with one or more pairs of ostia.

Excretory Organs.—In many larval Crustacea two pairs of modified segmental organs are present—the *antennary glands* opening on the bases of the antennæ, and the *maxillary* or *shell-glands* opening on the bases of the second maxillæ. But as development proceeds one pair nearly always atrophies, the maxillary gland alone being usually retained in the Branchiopoda, Ostracoda, Copepoda and Cirripedia, the antennary gland in the Malacostraca. In the Stomatopoda, however, there is no antennary gland, and the function of renal excretion may be discharged by a pair of glandular tubes opening into the rectum; and in Amphipoda, though antennary glands are present, an excretory function is also assigned to a cæcum or a pair of cæca opening into the posterior end of the mesenteron.

FIG. 406.—Nervous system of a Crab (**Maia squinado**). *bg.* thoracic ganglion; *cg.* commissural ganglion; *g.* brain; *m.* gizzard; *sc.* œsophageal connective; *sg.* visceral nerves; *y.* post-œsophageal connective. (From Lang's *Comparative Anatomy*, after Milne-Edwards.)

The **nervous system** is always formed on the ordinary arthropod type, as described in Apus and Astacus, and the chief variations it presents are connected with the greater or less amount of concrescence of ganglia. In the sessile Barnacles and in the Crabs (Fig. 406) this process reaches its limit, the whole ventral nerve-cord being represented by a single immense thoracic ganglion (*bg.*).

The **sense-organs** are mostly of the same character as those of the two examples. The median or nauplius-eye always occurs in the larva, and can frequently be shown to exist in the adult of even the higher groups (Decapoda). The Cirripedia and many parasitic Copepods are eyeless in the adult, as also are certain subterranean Malacostraca. Olfactory setæ occur, as a rule, on the antennules, and the statocysts of Decapoda are open sacs in the basal segment of the same appendages, but in Mysidacea they occur as closed cysts (Fig. 392, *ot.*) in the endopodites of the uropods.

Reproduction.—In most Crustacea the sexes are separate, but hermaphroditism occurs in some Branchiopods, in nearly all Cirripedes, and in certain

parasitic Isopods (*Cymothoa*). In the latter case the animals are protandrous, male organs being developed first, and female organs at a later stage. In many Cirripedia minute *complemental males* are found attached, like parasites, to the body of the ordinary or hermaphrodite individual, the male organs of which appear to be inadequate for the full discharge of the fertilizing function. Sexual dimorphism is almost universal, and reaches its maximum in the parasitic Copepods and Isopods already referred to.

The *gonads* are always a single pair of hollow organs discharging their products into a central cavity or lumen, whence they pass directly into the gonoducts and so to the exterior. The gonads may be simple or branched, and frequently there is more or less concrescence between those of the right and left sides, as in Astacus and Cyclops. The sperms vary greatly in form, and are usually motionless: in Cirripedia, however, they are motile, and in Ostracoda they perform movements after reaching the female ducts. In some Ostracoda they are about three times as long as the animal itself (Fig. 383, *D*). In many Branchiopoda and Ostracoda reproduction is parthenogenetic. In Daphnia, for instance, the animal reproduces throughout the summer by parthenogenetic *summer eggs* which develop rapidly in the brood-pouch (Fig. 382, 1, *br. p.*). In the autumn *winter eggs* are produced, which are fertilized by the males: they pass into the brood-pouch, a portion of which becomes specially modified and forms the *ephippium* or saddle. At the next moult the ephippium is detached and forms a sort of bivalved capsule in which the eggs remain in an inactive state during the winter, developing in the following spring.

Development.—In some Crustacea (*Lucifer*, *Euphausia*, and others) cleavage is complete, and a hollow blastula is formed: in others division of the nucleus into a number of daughter nuclei is followed by their migration towards the surface, where, each becoming surrounded by protoplasm, they form a layer of cells (blastoderm) enclosing a central mass of yolk (centrolecithal egg with superficial blastoderm): in others, again, the egg is telolecithal, and the protoplasm, accumulated at one pole, divides so as to form a disc of cells which afterwards spreads over the whole yolk.

Development is always accompanied by more or less metamorphosis. In most Branchiopoda the young is hatched in the form of a nauplius (Fig. 363, *A*), and further changes are of the same character as in Apus. In Cladocera development is direct, the nauplius-stage being passed through in the egg, and the young hatched in a form closely resembling the adult. In one of the Cladocera, however, *Leptodora* (Fig. 382, 3), while development of the summer eggs is direct, the winter eggs give rise to free nauplii. In the Ostracoda the nauplius is peculiar in having a bivalved shell and all three pairs of appendages uniramous. In all the Copepoda there is a free nauplius, which, in the parasitic forms, leads a free existence for a time, and then attaches itself to its particular host and undergoes retrograde metamorphosis.

In the Cirripedia, also, there is a free nauplius, the body of which is often produced into long spines. After several moults, the nauplius passes into a form called the *Cypris-stage* (Fig. 407), characterized by the presence of a bivalved shell, like that of an Ostracod: the antennules (*at.*[1]) have become modified into organs of adhesion by the development of the penultimate segment into a disc, the antennæ have disappeared, and six pairs of swimming-feet like those of a Copepod have made their appearance: there are paired compound eyes, and the shell is closed by an adductor muscle. After leading a free existence for a time, the Cypris-larva attaches itself by its antennules, aided by the secretion of cement-glands, and becomes a *pupa*: the carina, terga, and scuta appear beneath the shell, and within the skin of the mouth-parts and legs of the pupa appear the corresponding appendages of the adult. In Lepas the anterior region of the head grows out into a peduncle. The pupal integu-

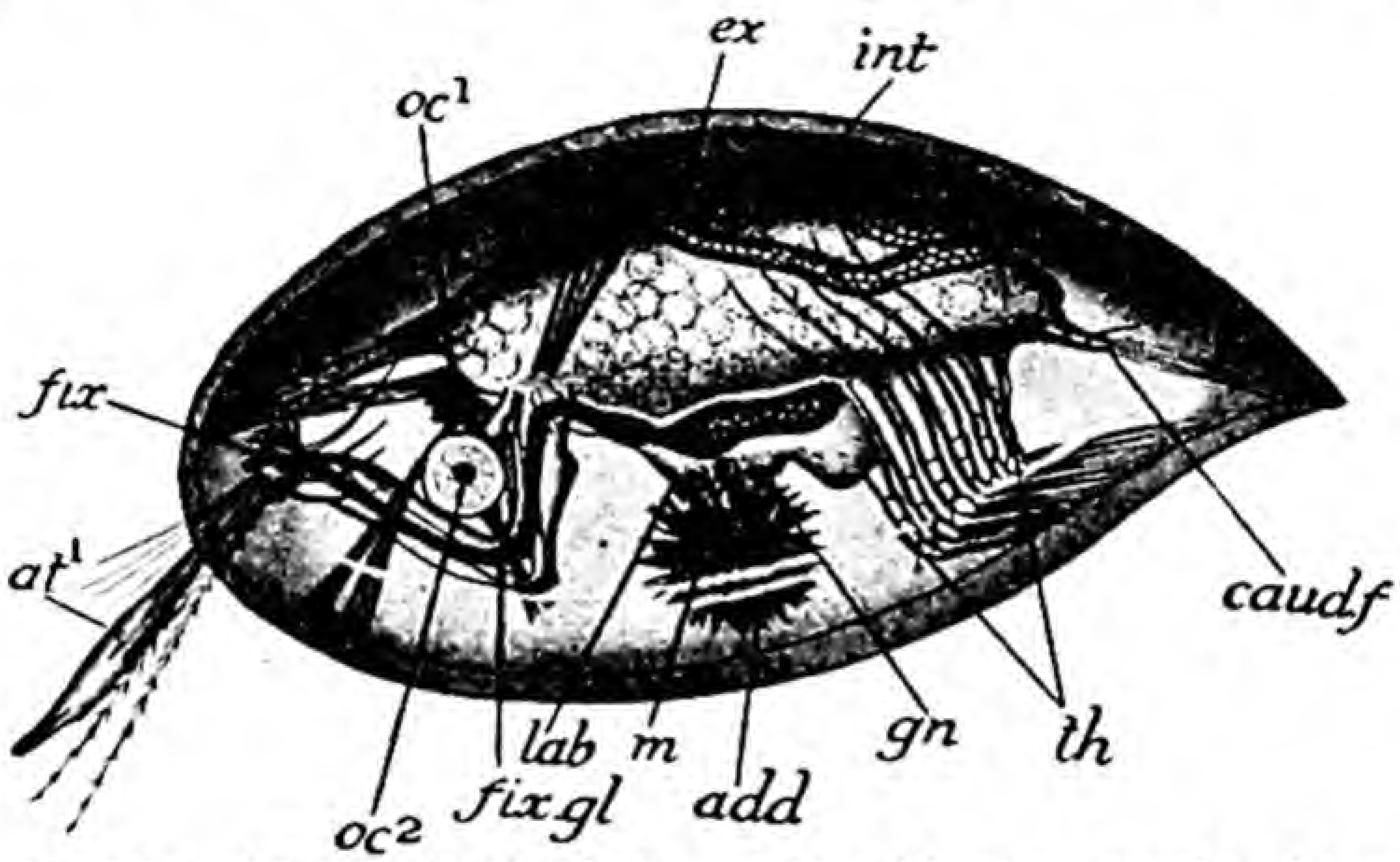


FIG. 407.—Cypris-stage of **Lepas fascicularis.** *add.* adductor muscle of carapace; *at.*[1], antennules; *caud. f.* caudal styles; *ex.* excretory organ (shell-gland); *fix.* disc for fixation; *fix. gl.* fixing gland; *gn.* jaws; *int.* intestine; *lab.* labrum; *m.* mouth; *oc.*[1], simple eye; *oc.*[2], compound eye; *th.* thoracic legs. (From MacBride, after Willemoes-Suhm.)

ment is then thrown off, the paired eyes disappear, and the adult form is assumed.

In Sacculina a still more extraordinary metamorphosis takes place. The young is hatched as a nauplius, but without alimentary canal, and passes into a Cypris-stage. In this condition, after a brief free existence, it attaches itself to the body of a young Crab, near the base of a seta, by means of its antennæ. The thorax with its appendages is thrown off, and the rest of the body is converted into a rounded mass of cells. The antennæ perforate the cuticle of the host, and, through the communication thus formed, the mass of cells passes into the interior of the Crab, and is carried by the movement of the blood until it comes to rest in the thorax. The Sacculina now sends out root-like processes, grows immensely, and, pressing upon the body-wall of the Crab, causes atrophy of the tissues: this allows the now greatly-swollen parasite to project on the exterior as the tumour-like adult described above (p. 435).

The embryo of Euphausia leaves the egg as a typical free-swimming nauplius; this passes into what is called the *protozoæa-stage*, distinguished by the possession of an elongated, unsegmented abdomen without appendages. After successive moults, the rest of the appendages appear, and the adult form is assumed. In Mysis (Fig. 392) the nauplius is maggot-like, and undergoes development in the brood-pouch, emerging in a condition closely resembling the adult.

The development of the Decapoda presents a very interesting series of modifications. In two genera of Prawns (*Penæus* and *Lucifer*) the embryo leaves the egg as a nauplius, and passes by successive moults through a proto-

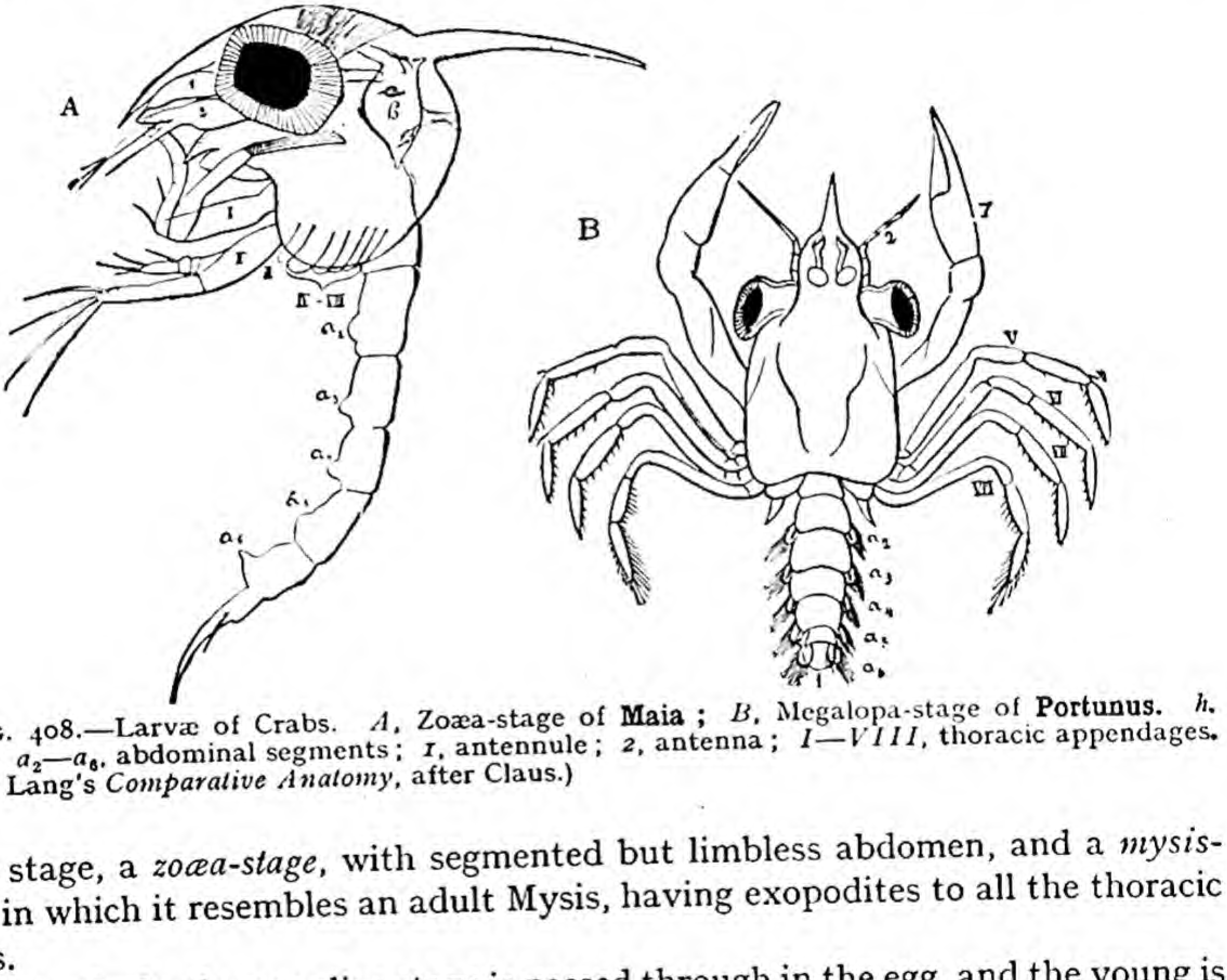


FIG. 408.—Larvæ of Crabs. *A*, Zoæa-stage of **Maia**; *B*, Megalopa-stage of **Portunus**. *h*, heart; a_2—a_6, abdominal segments; *1*, antennule; *2*, antenna; *I—VIII*, thoracic appendages. (From Lang's *Comparative Anatomy*, after Claus.)

zoæa stage, a *zoæa-stage*, with segmented but limbless abdomen, and a *mysis-stage* in which it resembles an adult Mysis, having exopodites to all the thoracic limbs.

In the Crabs the nauplius stage is passed through in the egg, and the young is hatched in the form of a peculiarly modified zoæa (Fig. 408, *A*), with an immense cephalothorax produced into spines, large stalked eyes, and a slender abdomen. This passes by successive moults into the *megalopa-stage* (*B*), which resembles an adult Macruran, having an extended abdomen with well-developed pleopods. The megalopa passes by successive moults into the adult form.

In the Lobster (*Homarus*) both nauplius and zoæa-stages are passed through in the egg, and the embryo is hatched in the mysis-stage with exopodites to all

the thoracic limbs. In the Rock-lobster (*Palinurus*), and its allies, the newly hatched young is a strangely modified mysis-form called a Glass-Crab or *Phyllosoma*: it has broad, depressed cephalic and thoracic shields of glassy transparency: the abdomen is very small and the legs extremely long and biramous. Lastly, in the Fresh-water Crayfish the young resemble the adult in all but proportions and certain unimportant details of structure. Thus in the series of Decapoda we get a gradual abbreviation in development, stages which are free larval forms in the lower types being hurried through before hatching in the higher.

The larvæ of Stomatopoda are grotesque little creatures with a very large spiny carapace. In Amphipoda there is no free larval form, but in Isopoda the young leave the egg in the form of a curious maggot-like modification of the nauplius, which remains in the brood-pouch until it has attained the adult form.

Mode of Life, etc.—The Crustacea are remarkable for their very perfect adaptation to the most various conditions of life: they occur in fresh-water, in the sea, in brine-pools, in subterranean caves, and on land: of the marine forms some are littoral, some pelagic, some abyssal, descending to over 3,000 fathoms. One species of Copepod, *Pontellina mediterranea*, may almost be considered as aërial: it is described as taking long flying leaps out of the water, after the manner of a Flying-fish. Some, like Lobsters, Crayfishes, etc., are solitary; others, like Shrimps, are gregarious, occurring in immense shoals. Most of them either prey on living animals or devour carrion, but, as we have seen, the Barnacles are fixed, and feed on minute particles after the fashion of many of the lower animals, and the members of more than one order are parasites remarkable for their deviation from the typical structure of the class and their adaptation to their peculiar mode of life. In size they present almost every gradation from microscopic Water-fleas to Crabs two feet across the carapace, or four feet from tip to tip of the legs.

As to geographical distribution, all the chief groups are cosmopolitan, and it is only among the families, genera, and species that matters of interest from this point of view are met with. Fossil remains are known from very ancient periods. The oldest forms are usually referred to the Leptostraca, and occur from the Cambrian to the Trias. The shells of Ostracoda are also known from the Cambrian upwards, and those of Cirripedia from the Silurian. Peracarida are known from Palæozoic times, but are rare as fossils: the earliest undoubted Macruran occurs in the Lower Trias, while the Brachyura are known from the Lower Oolite.

It was in the Crustacea that the recapitulation theory so often alluded to was first worked out in detail. Embryology shows that all Crustacea may be traced back in individual development to the nauplius, upon which follows some kind of zoæa-stage, many of the lower forms progressing no further. But in

Malacostraca the zoæa is followed by the mysis stage, which is permanent in the Mysidacea, transient in Decapods. It was certainly a tempting hypothesis that this series of forms represented as many ancestral stages in the evolution of the class. But we have to remember that all such free larvæ are subject to the action of the struggle for existence, and have no doubt been modified in accordance with their own special needs and without exclusive reference to their ancestors or to the adult species into which they finally change.

Many Crustacea present instances of *protective* and *aggressive characters*, *i.e.*, modifications in form, colour, etc., which serve to conceal them from their enemies or from their prey. Probably the most striking example is that of certain crabs (*Paramithrax*), which deliberately plant Sea-weeds, Sponges, Alcyonarians, Zoophytes, etc., all over the carapace, and are thus perfectly concealed except when in motion. Another Crab, a species of *Dromia*, carries a relatively immense Ascidian or Sea-squirt on its back, and in another member of the same family the hinder legs are used to hold umbrella-wise over the back a single valve of a bivalve shell.

Several instances of *commensalism* occur in the class. The association of Hermit-crabs with Sea-anemones, has already been referred to (p. 195): another interesting example is the occurrence of the little Pea-crab (*Pinnotheres*) in the mantle-cavity of Mussels. Other Decapods are found in the intestines of Sea-urchins and Holothurians, and one genus of Crab lives in a cavity in a Coral, the aperture being only just sufficient to allow of a due supply of food and water.

It is in Crustacea that we find the first indication of characters the purpose of which appears to be their attractiveness to the opposite sex. The immensely enlarged and highly coloured chelæ of some male crabs (*Gelasimus*, Fig. 402, 2) are said to be used for attracting the female as well as for fighting. The sound-producing organs of some Decapoda have probably also a sexual significance. The Rock-lobster (*Palinurus vulgaris*) has a soft chitinous pad on the antenna, which it rubs against a projecting keel on the sternal region of the head, producing a peculiar creaking sound; and *Alpheus*, another Macruran, makes noises by clapping together the fixed and movable fingers of its large chelæ. The fact that these sounds can be produced at the will of the animals seems to show that the latter undoubtedly possess a sense of hearing, and that the statocyst may also have an auditory function.

Affinities and Mutual Relationships.—That the Crustacea belong to the same general type of organization as the articulated worms is clear enough. The advance in structure is shown in the reduction in number and in the differentiation of the segments, and in the concrescence of those at the anterior end to form a head; in the hardening of the cuticle into sclerites so as to form a jointed armour; in the jointing and mobility of the limbs; and in the differentiation of the dorsal vessel into a heart by which the propulsion of the blood

is alone performed. The resemblance of the foliaceous limbs of Branchiopods to the parapodia of the higher worms is so striking that one can hardly believe it to be without significance. On the other hand, the absence of transverse muscles and of cilia, and the replacement of the cœlome by blood-spaces, are fundamental points of difference from any known Chætopod.

As to the mutual relations of the various orders, the Branchiopoda with their very generalized structure and parapod-like limbs, may be taken as the base of the series. The Ostracoda, Copepoda, Branchiura, and Cirripedia are best conceived as derivatives, along separate lines, of an ancestral form common to them and the Branchiopoda. By a differentiation of the post-cephalic limbs, and a reduction in the number of segments, the branchiopod type easily passes into that of the Leptostraca, which, though they nearly conform to the malacostracan type of segmentation, have still marked traces of relationship with lower groups in the presence of caudal styles and in their bivalved carapace and foliaceous thoracic appendages. Next to these in ascending order would come the Cumacea with their cephalic carapace coalescent with the first three of four thoracic segments and bounding branchial cavities at the sides of the thorax, but with—as more primitive features—a biramous character in some of the thoracic appendages and the absence of the fan-like tail-fin. Then a little higher, the Tanaidacea, Isopoda and Amphipoda and the Anaspidacea may be supposed to have branched off from the main trunk at about the same level, and may be regarded, on account of a number of resemblances, as having had a common origin from it. Probably the Anaspidacea are to be looked upon as more primitive than the other two groups in view of the less advanced coalescence of the first thoracic segment with the head, the absence of specialized maxillipeds, and the biramous character of the thoracic limbs; but, on the other hand, they show a higher development in the possession of the fan-like tail-fin and the stalked movable eyes such as characterize the Decapoda.

A stage nearer the latter group are the Mysidacea, with their single pair of maxillipeds, their stalked eyes, their rudimentary podobranchiæ and their fan-like tail-fin; but these still show some primitive features, more especially in their incomplete cephalothorax and their biramous thoracic appendages. But without doubt it is in the Euphausiacea that we find the nearest connections with the Decapoda. This is shown, in spite of the absence of maxillipeds, in their completed cephalothorax, their series of podobranchiæ, and sac-like heart, in addition to their stalked eyes and fan-like tail-fin.

From the Euphausiacea the Macrura are derivable by the differentiation of three pairs of foot-jaws and the disappearance of the exopodites of the legs. In the series of the Macrura we find, on passing from the Prawns through such forms as Astacus, Palinurus, and Scyllarus, a gradual shortening of the abdomen, accompanied by a broadening and flattening of the whole body. In

Birgus, Hippa, etc., this process goes a step further, and the abdomen becomes permanently flexed under the cephalothorax, thus leading to the high degree of specialization found in the Crabs.

APPENDIX TO CRUSTACEA.

The Trilobita.

The Trilobita are extinct Arthropods peculiar to, and characteristic of, the Palæozoic rocks: they are specially abundant from the upper Cambrian to the Carboniferous. They are often found in a wonderfully good state of preservation, owing to the hard exoskeleton covering the dorsal surface: the greater part of the ventral region and the

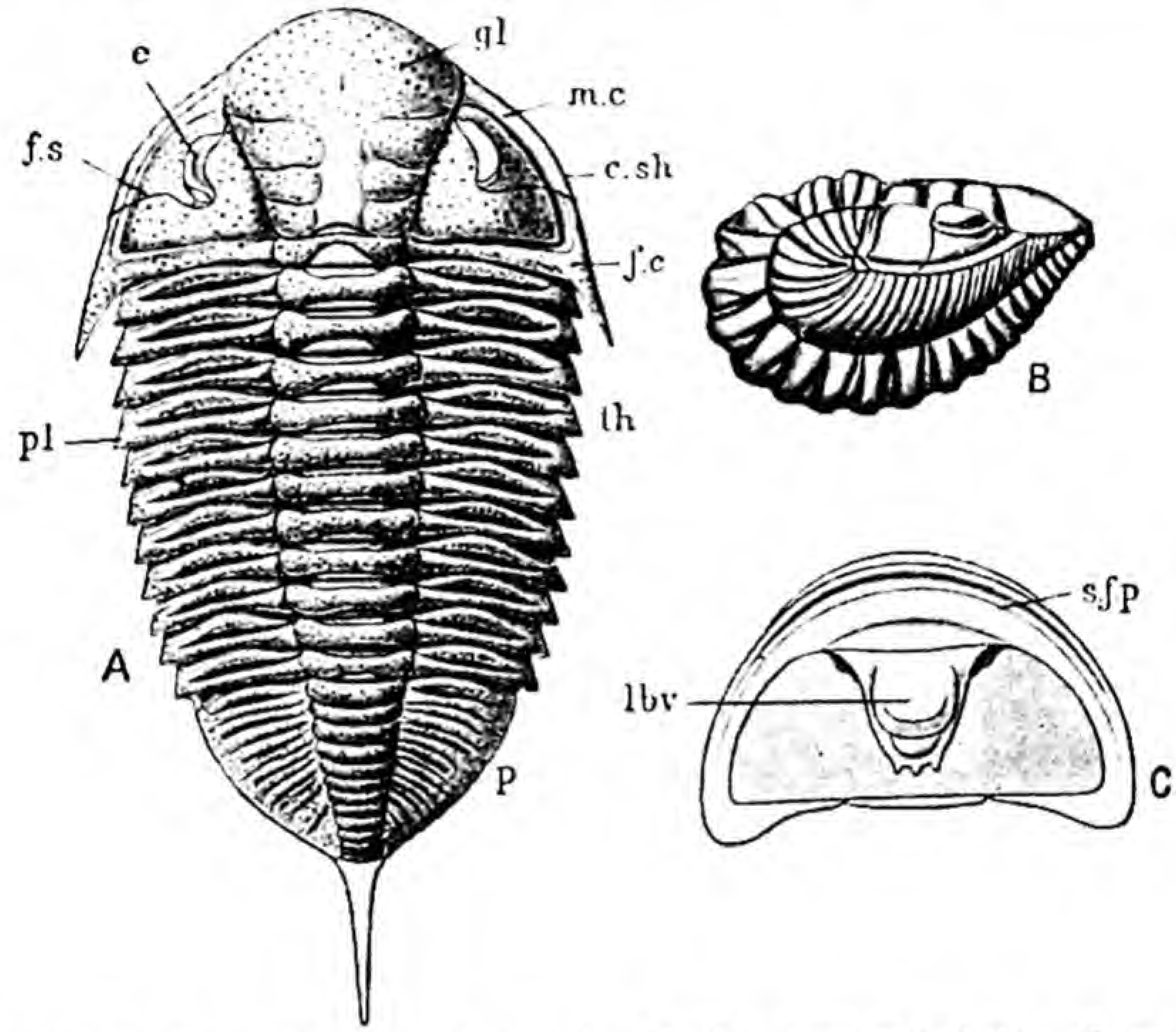


Fig. 409.—**Dalmanites socialis,** dorsal aspect; *B*, the same rolled up; *C*, under-side of head of **Phacops fecundus.** *c. sh.* cephalic shield; *e.* eye; *f. c.* fixed cheek; *f. s.* frontal suture; *gl.* glabella; *lbv.* labrum; *m. c.* movable cheek; *p.* pygidium; *pl.* pleura; *s. f. p.* sub-frontal plate; *th.* thorax. (After Gerstaecker.)

appendages were, however, very delicate, and are preserved only in exceptionally favourable cases.

The body is depressed, more or less oval in outline, and divided into three regions, the *head* (Fig. 409, *c. sh.*), the *thorax* (*th.*), and the *abdomen* (*p.*), all of which usually present an elevated median ridge and depressed lateral portions, whence the trilobation generally characteristic of the group. The head is covered by a carapace or *cephalic shield* (*c. sh.*), the elevated median region of which, known as the *glabella* (*gl.*), usually presents three or four transverse grooves, probably indicating the presence of four or five segments. The lateral regions of the carapace are divided by an oblique line of separation, the *frontal* or *facial suture* (*f. s.*), into an inner or mesial portion, the *fixed cheek* (*f. c.*), continuous with the glabella, and an outer free portion, the *movable cheek* (*m. c.*); the latter bears the large paired compound eye (*e.*). In some cases there is an indication of a dorsal organ, like that of Apus, on the last cephalic segment. Ventrally the carapace is continued, as in Apus, into a sub-frontal plate (*C, s. f. p.*), to the posterior edge of which is attached a

large labrum or hypostome (*lbv.*). In many Trilobites the hypostome bears a pair of small compound eyes. The posterior angles of the carapace are often produced into spines.

The thorax (*th.*) is composed of a variable number (2–29) of movably articulated segments, which are commonly trilobed, consisting of a median region or *axis*, and of lateral *pleura* (*pl.*) often produced backwards and downwards into spines. The abdomen is covered by a *caudal shield* or *pygidium* (*p.*), formed of a variable number of fused segments. Owing to the mobility of the thorax, the Trilobites were able in many cases to roll themselves up like Wood-lice (*B*). Each of the segments, with the sole exception of the last or anal, bore a pair of appendages.

The appendages are known only in a few cases. Quite recently a single pair of antennæ

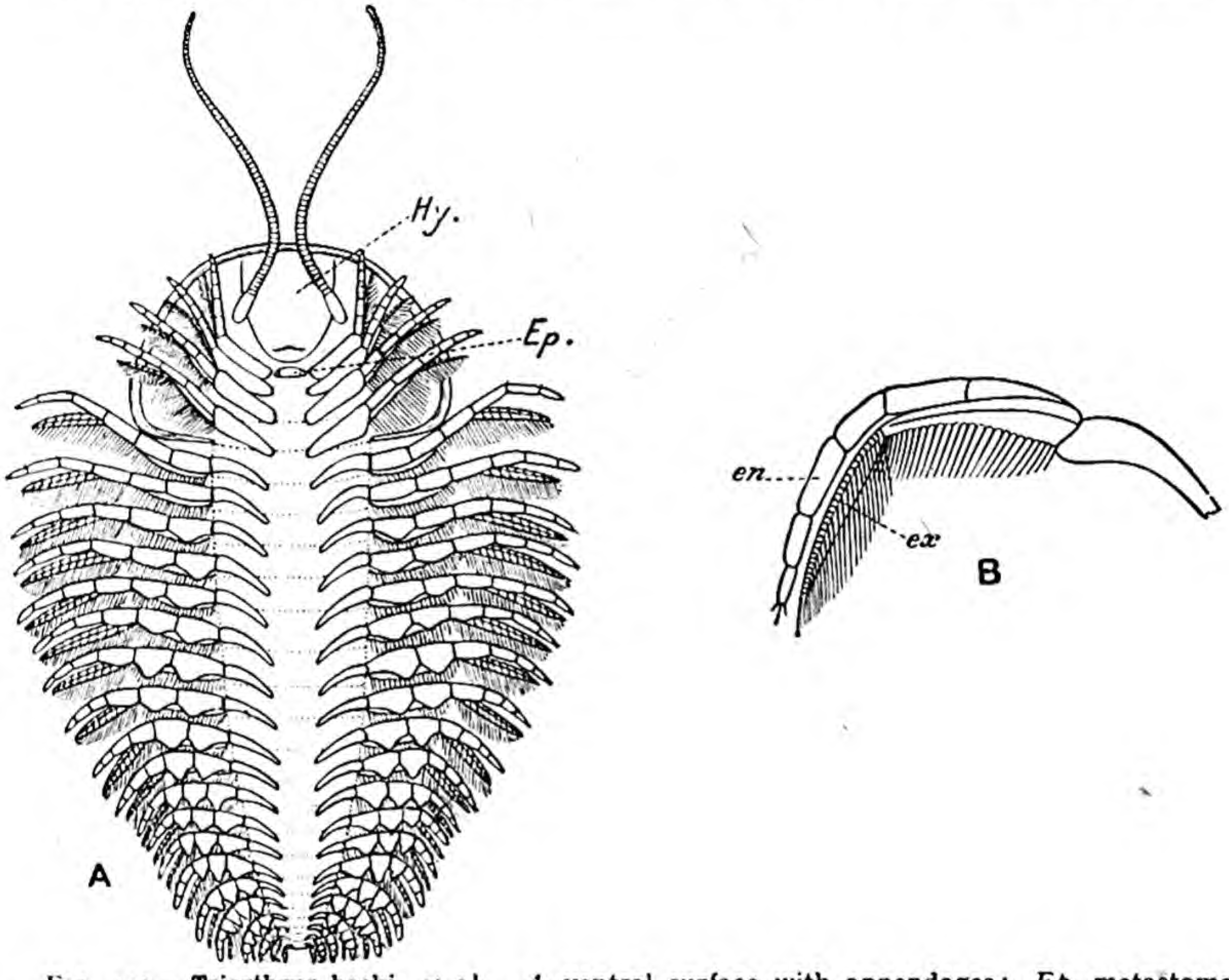


FIG. 410.—**Triarthrus becki,** × 2½. *A*, ventral surface with appendages; *Ep*, metastome; *Hy*, hypostome. *B*, second thoracic appendage. *en*. endopodite; *ex*. exopodite × 12. (From the *Cambridge Natural History* after Beecher.)

(Fig. 410) has been shown to exist in one species, probably attached to the sub-frontal plate. There are no true jaws. Four pairs of biramous leg-like cephalic appendages have been demonstrated, and the thorax bears slender biramous legs with endo- and exo-podites, and bearing spiral gills. Similar limbs are present on the abdomen.

The larvæ of several species of Trilobites have been found in the fossil state. In some of these stages the body consists only of carapace and pygidium in the youngest, and the thoracic segments are subsequently intercalated in regular order. In other species the earliest stage has the form of a rounded plate, the posterior portion of which elongates and segments to form the thorax and abdomen. Nothing is known of the larval appendages, and none of the stages hitherto discovered can be considered as nauplii.

The precise systematic position of the Trilobites is uncertain, but their nearest affinities seem to be, on the whole, with such Branchiopoda as Apus; the relationship is, however, by no means a close one.

CLASS II.—MYRIAPODA.

The class Myriapoda, including the Centipedes and the Millipedes, consists of tracheate Arthropoda, which present many features of resemblance to the Insects. There is a distinct head, bearing many-jointed antennæ, a pair of eyes, and two or three pairs of jaws; the body is not distinguishable into regions, but consists of a number of similar segments, each bearing either one pair of legs or two pairs. A system of air-tubes or tracheæ, similar to those of Peripatus and the Insects, opens by a series of stigmata usually in considerable numbers, on the sides or lower surfaces of the segments.

As will appear subsequently, the class Myriapoda, as formerly understood, comprises two groups which are separated from one another by such important differences that they might very well be looked upon as constituting two distinct and independent classes. The old class Myriapoda is retained here as a matter of convenience, and the two constituent groups are ranked as sub-classes.

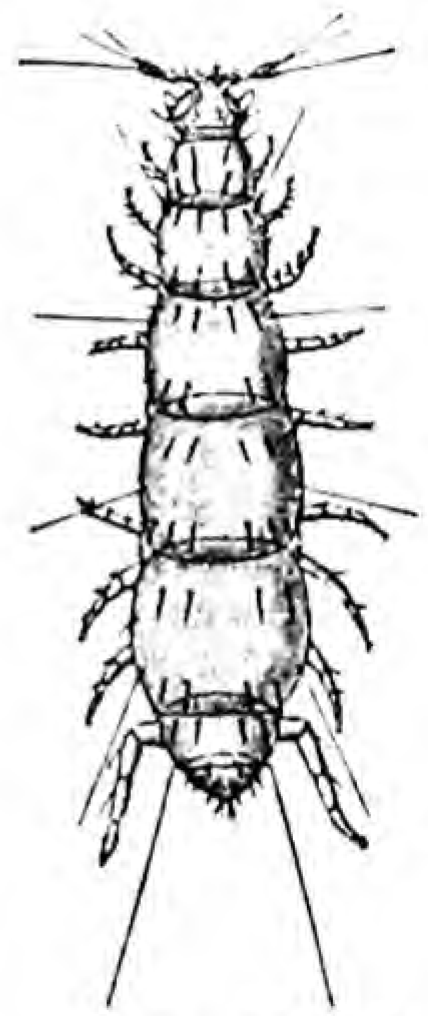


FIG. 411.—**Pauropus huxleyi.** (From Leuckart, after Latzel.)

Sub-Class I.—Progoneata.

"Myriapoda" in which the genital apertures are situated far forwards towards the anterior end of the body.

ORDER 1.—PAUROPODA.

Progoneata with eleven trunk segments and an anal pygidium; nine pairs of legs; the first trunk segment with a pair of rudimentary legs, the last trunk segment and the pygidium without appendages; the head with antennæ, one pair of mandibles, and only one pair of maxillæ; antennæ with three flagella and auditory (?) organ; without tracheæ and blood system.

The order includes three families: the *Brachypauropodidæ*, the *Pauropodidæ* (*Pauropus*) (Fig. 411), and the *Eurypauropodidæ*.

ORDER 2.—DIPLOPODA.

Progoneata with a body composed of a considerable number of apparent segments, each of which, with the exception of the first four, bears two pairs

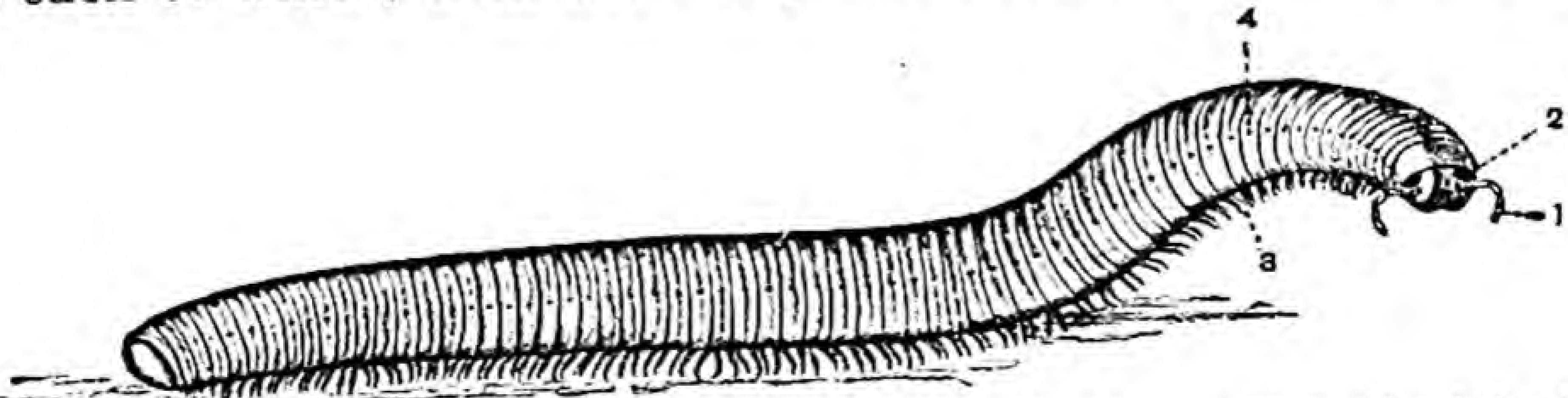


FIG. 412.—**Iulus terrestris.** 1, antenna; 2, eye; 3, legs; 4, pores, of stink-glands. (From Shipley and MacBride's *Zoology* (University Press, Cambridge), after Koch.)

of legs and represents two united true segments; head with antennæ, one pair of mandibles, and only one pair of maxillæ forming the so-called gnathochilarium.

This order includes the *Millipedes*. One of the commonest of the 900 genera of this order is *Iulus* (Fig. 412).

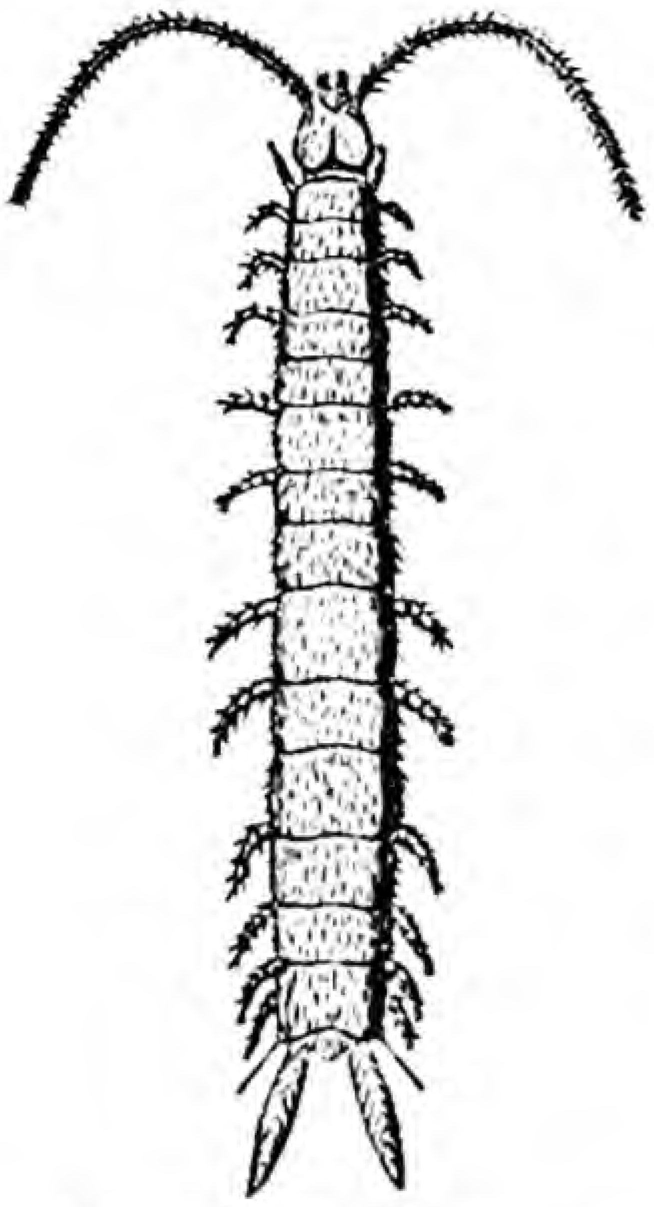


FIG. 413.—**Scolopendrella immaculata.** (From Leuckart, after Latzel.)

ORDER 3.—SYMPHYLA.

Progoneata with not more than twelve leg-bearing segments; head with antennæ, one pair of mandibles, and two pairs of maxillæ; feet with two claws; there is only a single pair of branching tracheæ, the two external apertures of which are situated in the head.

This order includes the genera *Scolopendrella* (Fig. 413) and *Scutigerella*.

Sub-Class II.—Opisthogoneata.

"Myriapoda," in which the genital apertures are situated at the posterior extremity of the body.

ORDER 1.—CHILOPODA.

Opisthogoneata with numerous (15–177) trunk segments, each bearing a single pair of legs; head with antennæ, one pair of mandibles, and two pairs of maxillæ; second maxillæ usually fused to form a labium; the first pair of trunk appendages, the maxillipeds, bear a sharp claw which is connected with a poison gland; feet with a single claw; numerous tracheæ opening in pairs of stigmata on the sides of a number of the segments.

This order includes the *Centipedes*. Examples: *Scolopendra* (Fig. 414), *Lithobius* (Fig. 415), and *Scutigera*.

GENERAL ORGANIZATION.

External Features.—The *head* in the Myriapoda is well marked off; it is composed of six fused segments. The *antennæ* consist sometimes of many, sometimes of comparatively few segments; in *Pauropus* they are branched. A pair of *eyes*, situated on the dorsal surface of the head, consist of aggregations of ocelli except in *Scutigera*, in which there are pseudo-compound eyes. There are a pair of *mandibles*, and one or two pairs of *maxillæ*. The mandibles have no palps; one or both pairs of maxillæ usually possess palps; the second pair of maxillæ are in some groups more or less united together. In the Chilopoda the first pair of legs of the trunk are specially modified to act as

poison-jaws (maxillipeds), by means of which the Centipede inflicts its poisonous bite.

The number of segments in the body varies from 11 to 177. In the Millipedes the dorsal walls of the segments are very strongly arched; in the Centipedes the segments are all dorso-ventrally compressed, with distinct tergal

FIG. 414.—**Scolopendra.** (From Cuvier's *Animal Kingdom.*)

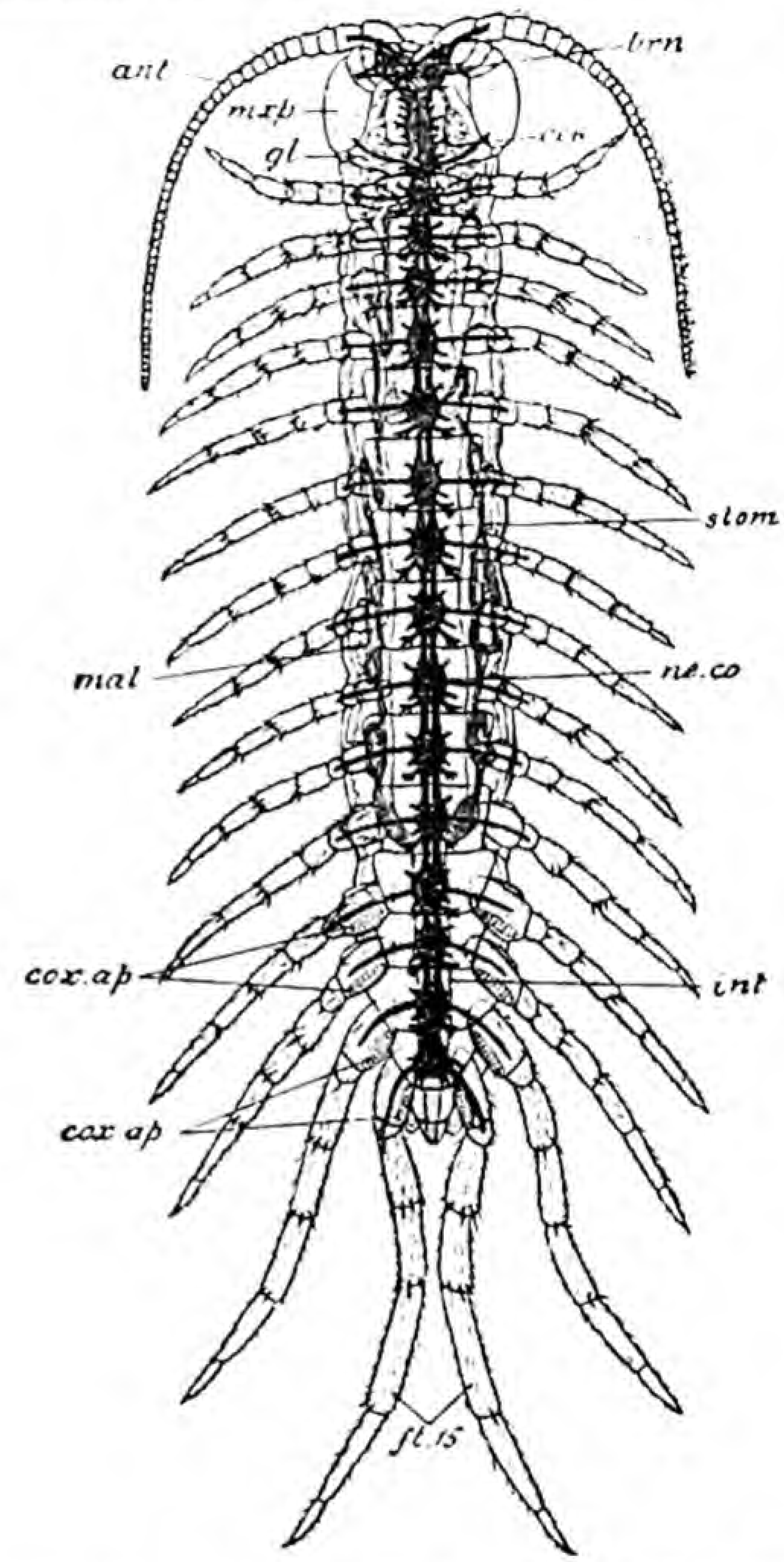


FIG. 415.—**Lithobius forficatus** seen from the ventral side. *ant.* antennæ; *brn.* brain; *cox. ap.* coxæ of appendages; *ft.* 15, fifteenth pair of legs; *int.* intestine; *mal.* Malpighian tubes; *mxp.* maxillipeds; *ne. co.* nerve cord; *œs.* œsophagus; *stom.* stomach. (From Leuckart.)

and sternal shields separated laterally by intervals of comparatively soft skin on which the stigmata open. In the Chilopoda each segment bears a pair of jointed legs; of these the most anterior pair is extended forwards, as already stated, to form a pair of poison-jaws (*maxillipeds*), at the extremity of the pointed terminal joint of which opens the duct of a poison-gland. In

the Diplopoda each segment behind the fourth bears two pairs of legs, the second, third, and fourth having only one pair each. In most of the Diplopoda the appendages of the seventh segment are modified in the male to form copulatory organs.

The **integument** and **body-wall** do not differ widely from those of Insects (see p. 490). The exoskeleton is a thickened chitinous cuticle which is calcified in Diplopoda. Odoriferous glands are present in most Diplopoda on some of the body-segments, and open on the dorsal surface. *Scolopendrella* possesses spinning glands.

The **alimentary canal** is straight. There are salivary glands, and one or two pairs of *Malpighian tubes*, having a renal function, open into the beginning of the hind-gut.

The **heart** is a greatly elongated tube, divided into a number of chambers.

The **respiratory system** resembles that of Insects, which will be fully dealt with later, consisting of air-tubes or *tracheæ*. There is one pair of stigmata in each true segment in the Diplopoda (two pairs in each apparent segment). Each stigma leads into an air-chamber from which a large number of tracheæ are given off. In some Diplopoda the tracheæ are branched, in others unbranched: the tracheæ of one group do not anastomose with those of other groups. In the Chilopoda the number of stigmata is in most cases less than the number of segments, and the tracheæ anastomose, often forming longitudinal trunks which may extend throughout the body. In *Scutigera* the stigmata are unpaired and dorsal, and each leads into a large air-chamber which gives off on either side a large number of radially arranged short air-tubes—the whole forming a sort of lung.

In the Symphyla there are only two stigmata, and these are situated on the head.

The **nervous system** consists of a brain, a pair of œsophageal connectives, and a ventral nerve-cord consisting of a series of double nerve-ganglia, one in each segment, with double connectives between them. The double character of the ventral cord is much more distinctly marked in the Chilopoda than in the Diplopoda, the ganglia are more distinct, and the first three are intimately united together into an infra-œsophageal mass. A sympathetic or visceral nervous system is present.

The **sexes** are always separate. There is usually an unpaired gonad with paired ducts. In the Chilopoda the single genital aperture is situated at the posterior end of the body: in the Diplopoda and Pauropoda the two apertures are placed far forwards towards the anterior end.

The **ovum,** as in most Arthropods, contains a large quantity of food-yolk. The centrally-placed zygote-nucleus divides so as to give rise to a number of nuclei, this division being accompanied by a partial division of the yolk into a number of masses. The nuclei then, for the most part, migrate to the

being folded up like a fan beneath the anterior pair; generalized biting mouth-parts; abdomen usually with cerci of varying character; incomplete metamorphosis.

This order is subdivided into the following sub-orders:

Sub-order a.—*Saltatoria.*

Orthoptera in which the last pair of legs is modified for jumping; including the *Grasshoppers, Locusts*, and *Crickets* (Fig. 435 a, b).

Sub-order b.—*Phasmida.*

Curiously modified Orthoptera, which closely similate sticks, grass stems, or leaves (*Stick-* and *Leaf-Insects*, Fig. 435, c, d).

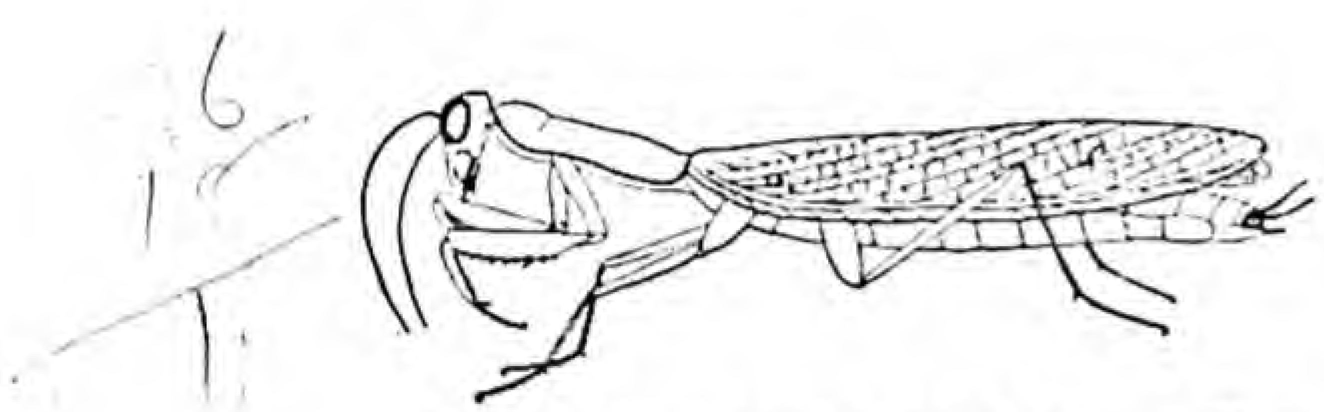


FIG. 436.—**Mantis religiosa.** (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

FIG. 437.—**Forficula auricularia;** male with right wing extended. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Chopard.)

Sub-order c.—*Mantoda.*

Orthoptera in which the first pair of legs is modified for the capture of animal prey; at rest these powerful raptorial organs are raised together in front (*Praying Insects*, Fig. 436).

Sub-order d.—*Blattaria.*

Orthoptera in which the three pairs of legs are very much alike. This sub-order comprises the *Cockroaches* which are swift runners. Example: *Blatta* (Fig. 417).

ORDER 2.—DERMAPTERA.

Exopterygota with two pairs of wings; anterior wings modified into short tegmina; posterior wings membranous with radially disposed veins; mouth-parts biting; cerci modified into forceps; metamorphosis slight or wanting.

This order comprises the *Earwigs* (Fig. 437).

ORDER 3.—ISOPTERA.

Social and polymorphic Exopterygota; communities composed of winged and wingless sexual individuals, and wingless sterile soldiers and workers; the two pairs of wings are very similar, capable of being shed; mouth-parts biting; metamorphosis slight or absent.

This order comprises the *Termites* or "*White Ants*" (Fig. 438).

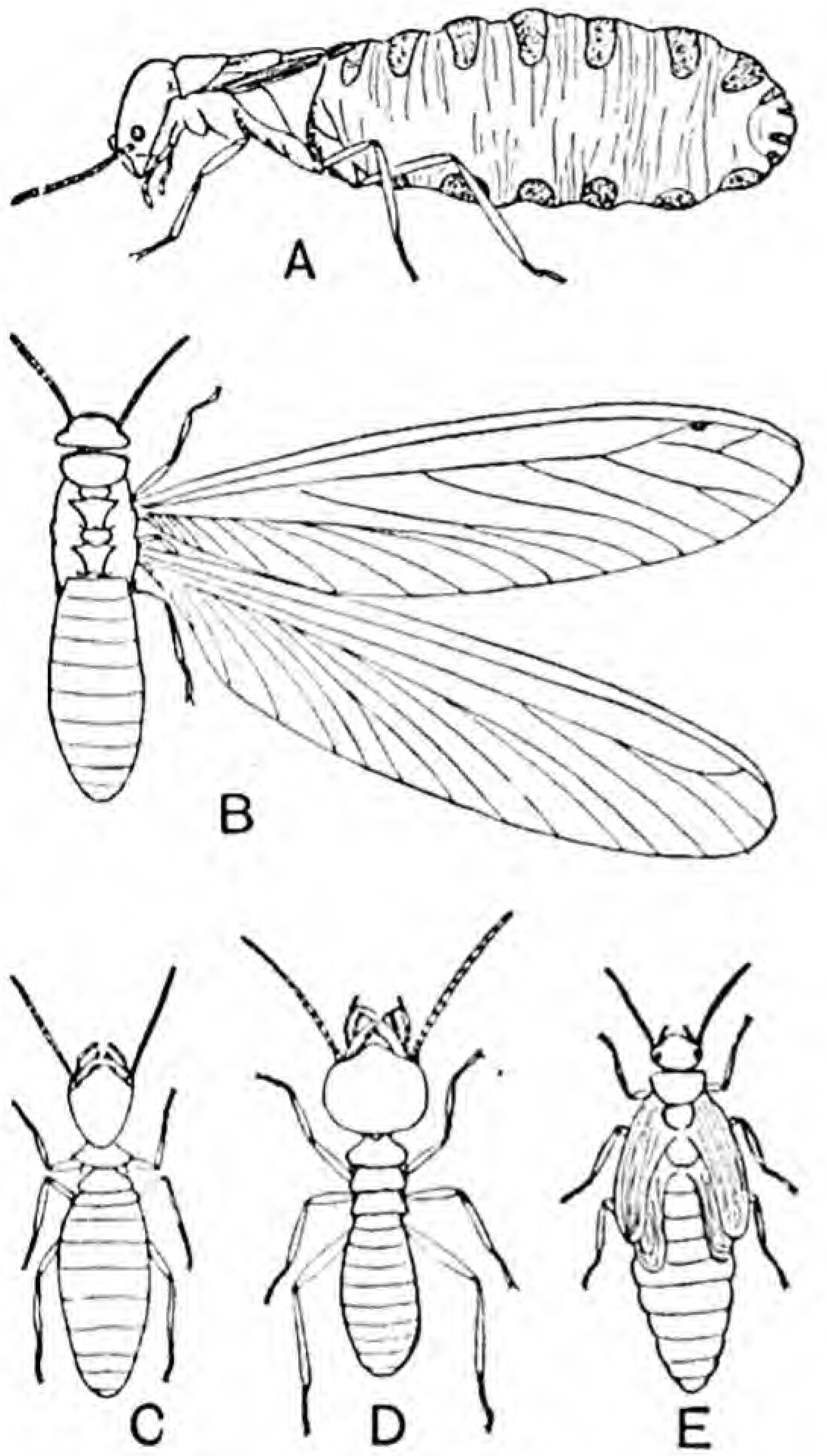


FIG. 438.—**Hamitermes silvestri** Hill. (From Borradaile, Eastham, Potts, and Saunders's *The Invertebrata* (University Press, Cambridge), after Tillyard.)

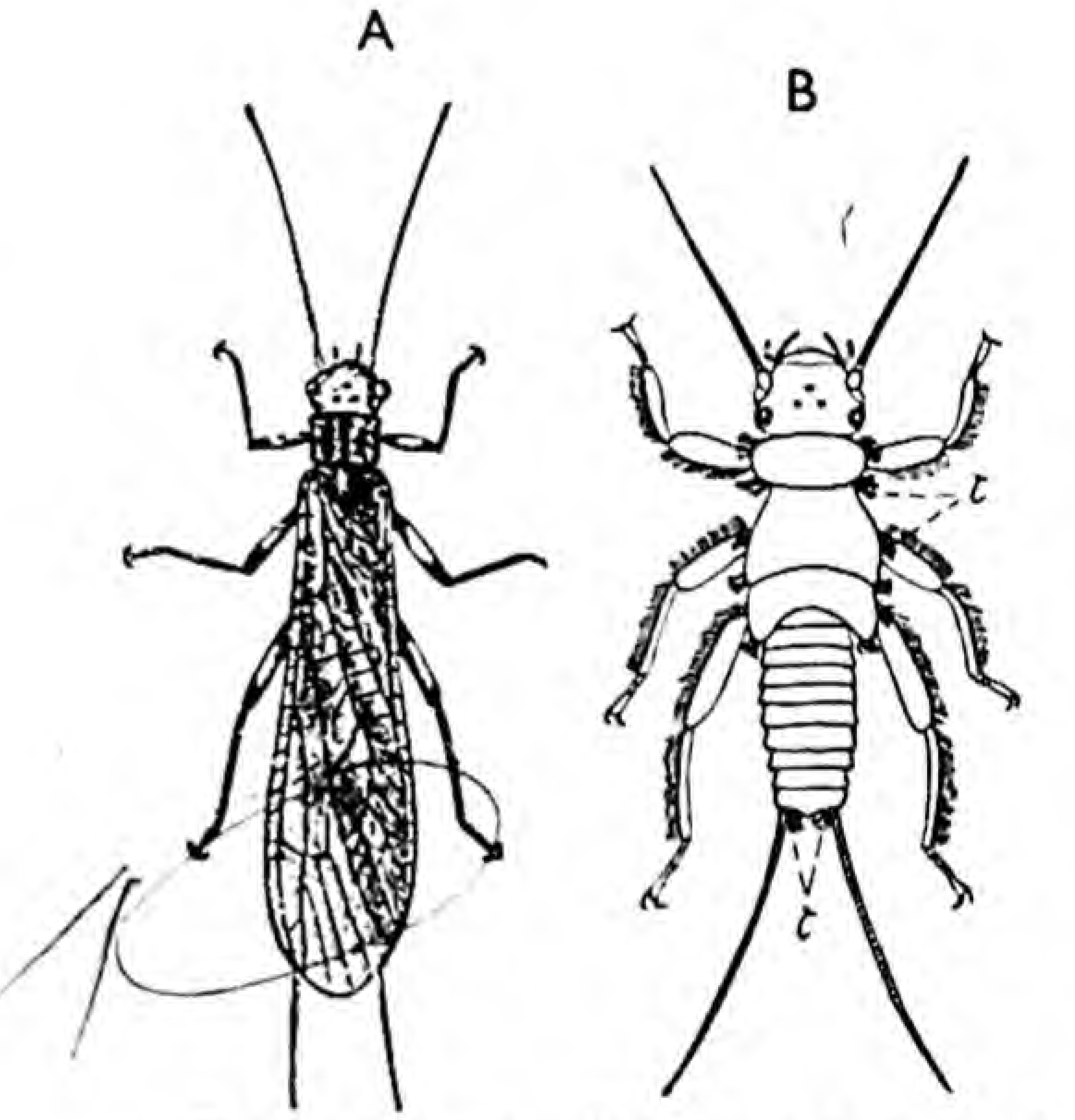


FIG. 439.—*A*, **Perla maxima**; *B*, **Nymph of Perla sp.**; *t*. tracheal gills. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), *A*, after Pictet).)

ORDER 4.—PLECOPTERA (PERLIDÆ).

Exopterygota with two pairs of wings held flat over abdomen at rest, posterior pair usually larger; elongate antennæ; mouth-parts biting; abdomen usually with long cerci; metamorphosis incomplete; aquatic nymphs usually with tracheal gills.

This order comprises the *Stone-flies* (Fig. 439, A, B).

ORDER 5.—EMBIODEA.

Exoptergyota with two pairs of wings of equal size; females always, males sometimes wingless; antennæ elongate; mouth-parts biting; metamorphosis gradual in male, absent in female (*Oligotoma*, Fig. 440).

ORDER 6.—PSOCOPTERA.

Winged or wingless Exopterygota of very small size; wings, when present, membranous, anterior pair larger; mouth parts biting; metamorphosis gradual or wanting.

There are two sub-orders, viz. a. the *Zoraptera* (only one genus known); b. the *Psocida*, including the *Book-lice* and their allies (*Psocus*, Fig. 441).

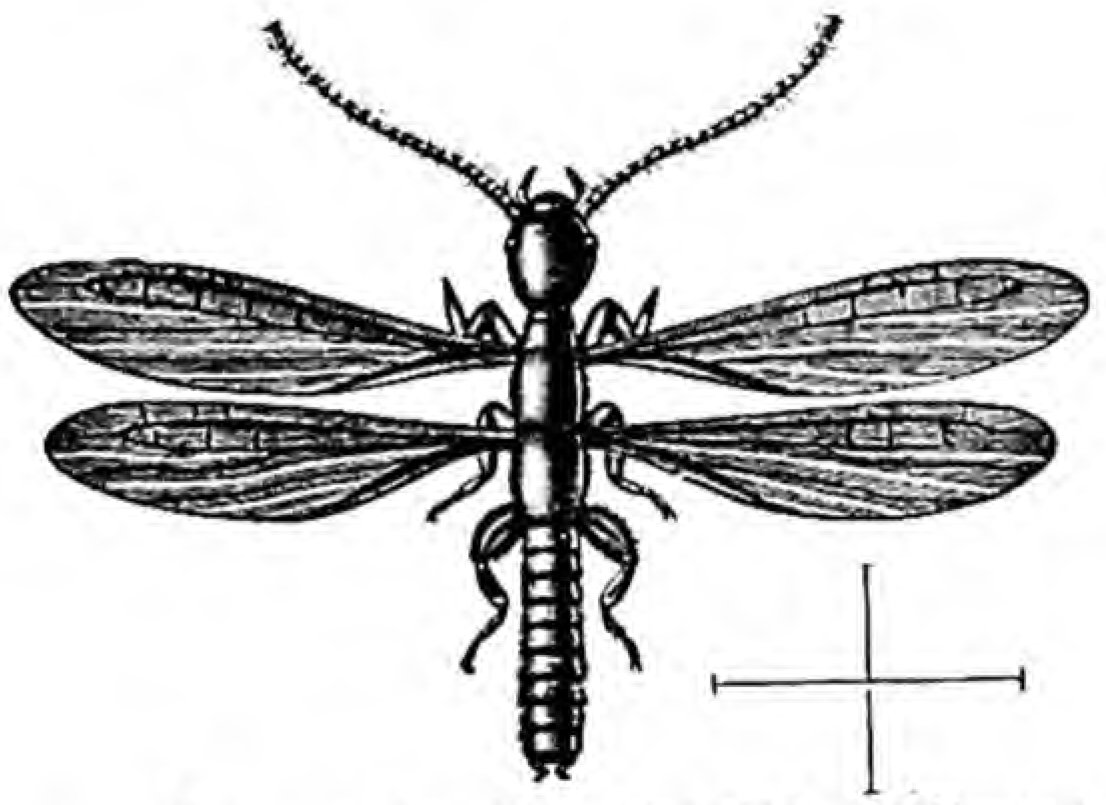


FIG. 440.—An **Embiid** (*Oligotoma michaeli*) magnified. (From the *Cambridge Natural History*, after MacLachlan).

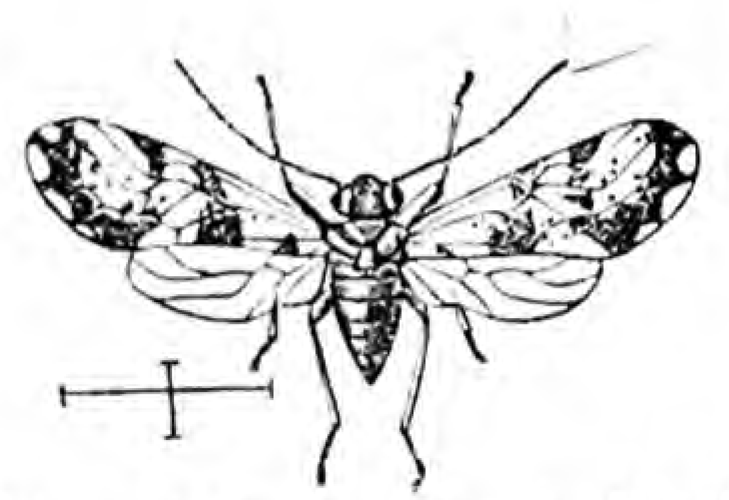


FIG. 441.—A winged Psocid (**Psocus fasciatus**), magnified. (From the *Cambridge Natural History*, after MacLachlan.)

ORDER 7.—EPHEMERIDA.

Exopterygota with two pairs of wings, held vertically upwards at rest, hind pair considerably reduced; antennæ short; mouth-parts vestigial; abdomen with very long cerci and often with a median caudal filament; metamorphosis incomplete; nymphs aquatic, with tracheal gills.

This order comprises the *May-flies* (Figs. 442, 443).

ORDER 8.—ODONATA.

Exopterygota with two equal or nearly equal pairs of wings; antennæ very short; mouth-parts biting; eyes very large and prominent; metamorphosis incomplete; aquatic nymphs with rectal or caudal gills and a powerful prehensile labium.

This order comprises the *Dragon-flies* (Figs. 444, 445).

ORDER 9.—HEMIPTERA (RHYNCHOTA).

Exopterygota in which two pairs of wings are usually present, sometimes similar, sometimes dissimilar, and in which there is a jointed suctorial rostrum formed from the labium, enclosing the jaws in the form of piercing organs; the prothorax is free from the other segments of the thorax; metamorphosis incomplete.

This order is subdivided into two sub-orders, viz. a. the *Heteroptera* (*Bugs*,

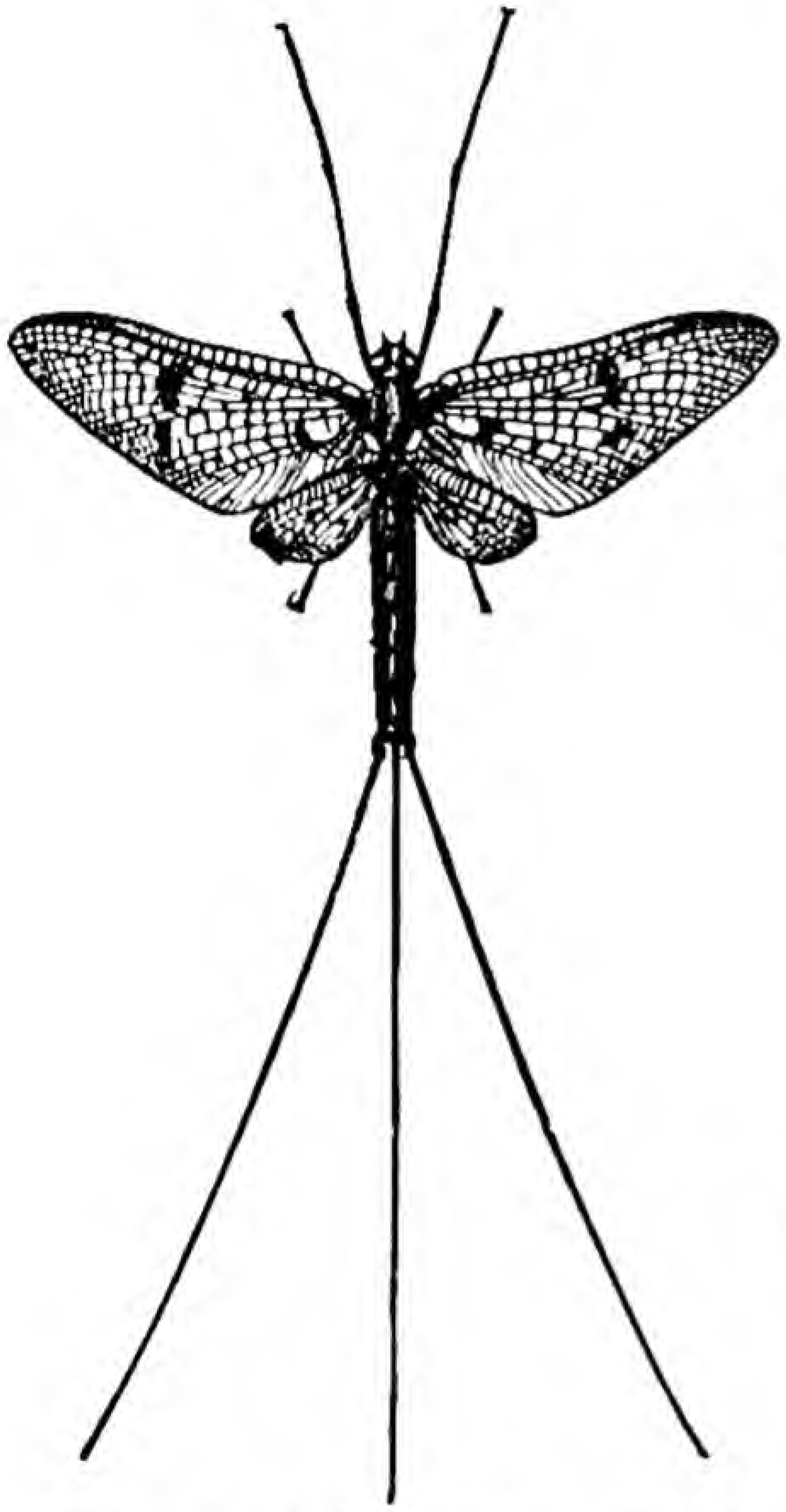


FIG. 442.—**Ephemera vulgata.** From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

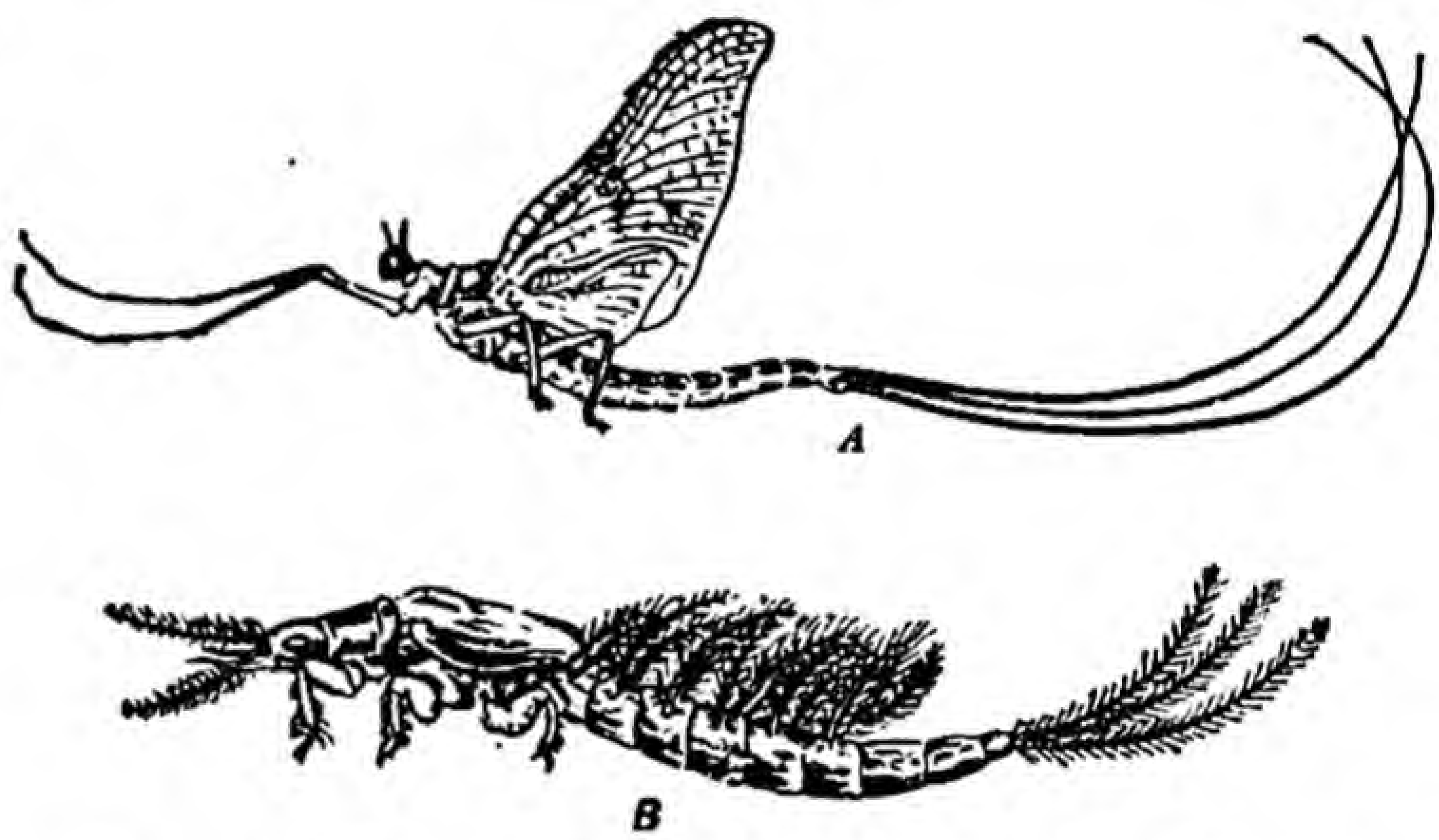


FIG. 443.—Metamorphosis of Ephemera. *A*, male imago; *B*, nymph. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Needham.)

Fig. 446, and *Water-bugs*, Fig. 447); b. the *Homoptera* (*Cicadas*, Fig. 448, *Plant-lice*, Fig. 449, and *Scale-insects*, Fig. 450).

ORDER 10.—MALLOPHAGA.

Small, flat, secondarily wingless Exopterygota with biting mouth-parts; metamorphosis absent.

This order comprises the *Biting Lice* or *Bird-lice*, which are external parasites

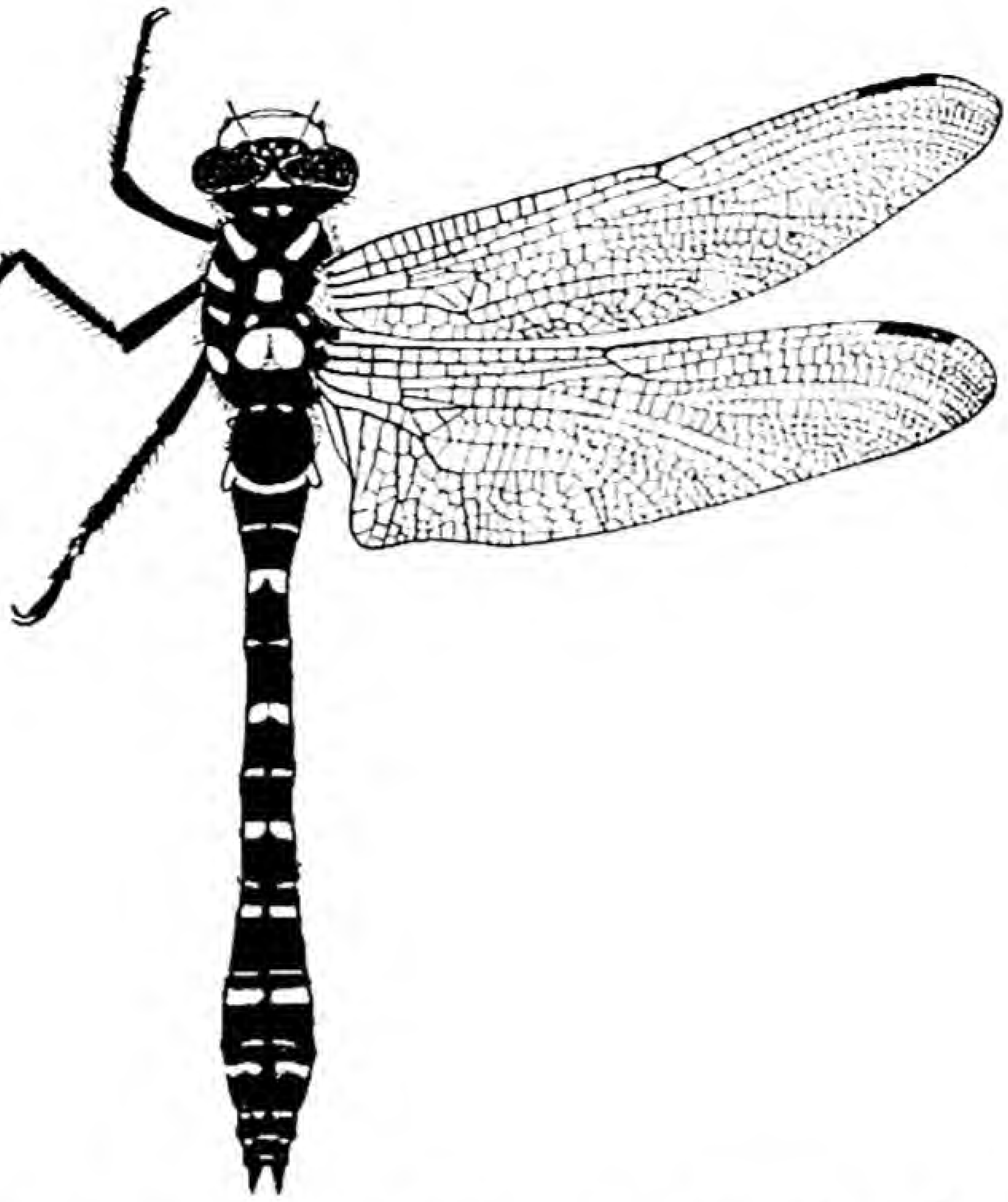


FIG. 444.—**A Dragon-fly (Cordulegaster annulatus),** male. (From Imms's *A General Textbook of Entomology* (Methuen & Co. Ltd.).)

FIG. 445.—**A Dragon-fly nymph (Anax imperator)** with mask extended and seizing prey. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Lucas.)

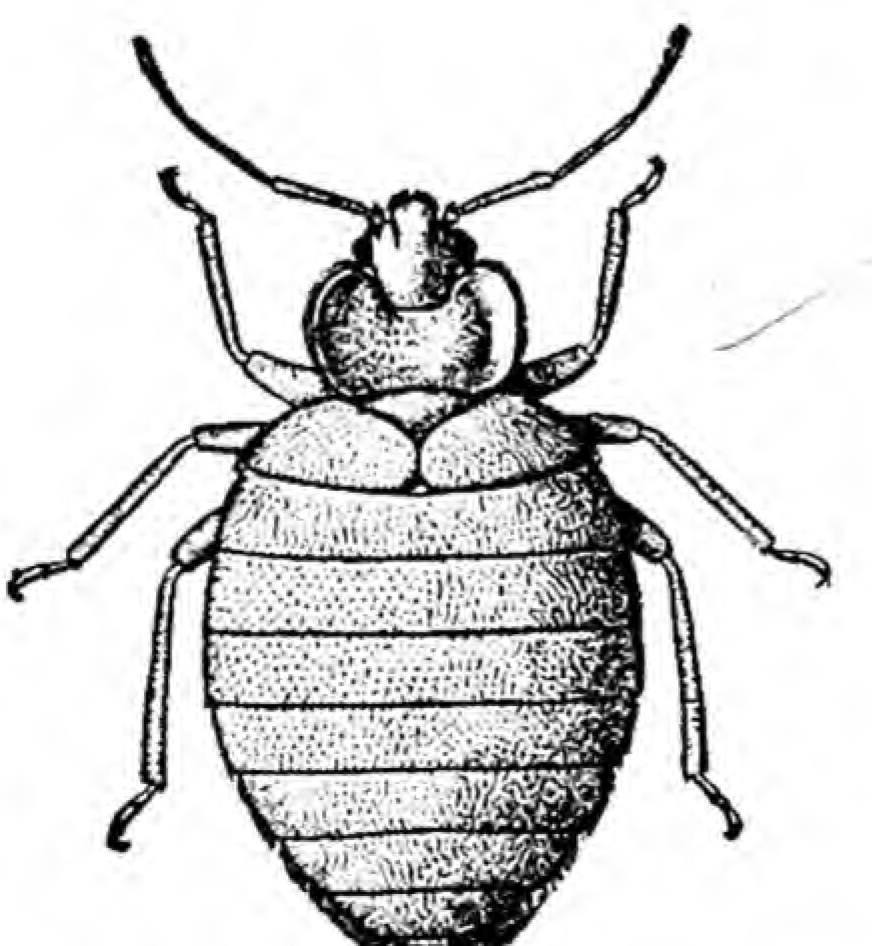


FIG. 446.—**Bed Bug (Cimex lectularius)**, male. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

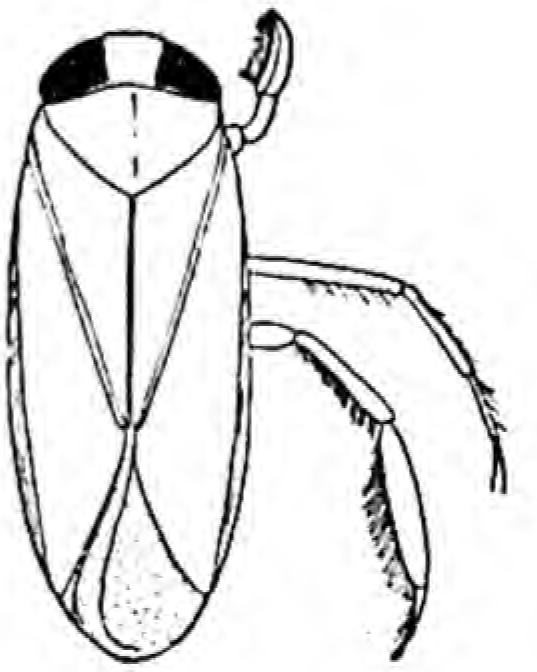


FIG. 447.—**Water-bug (Corixa)**. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

FIG. 448.—**Cicada.** (After Guèrin and Percheron.)

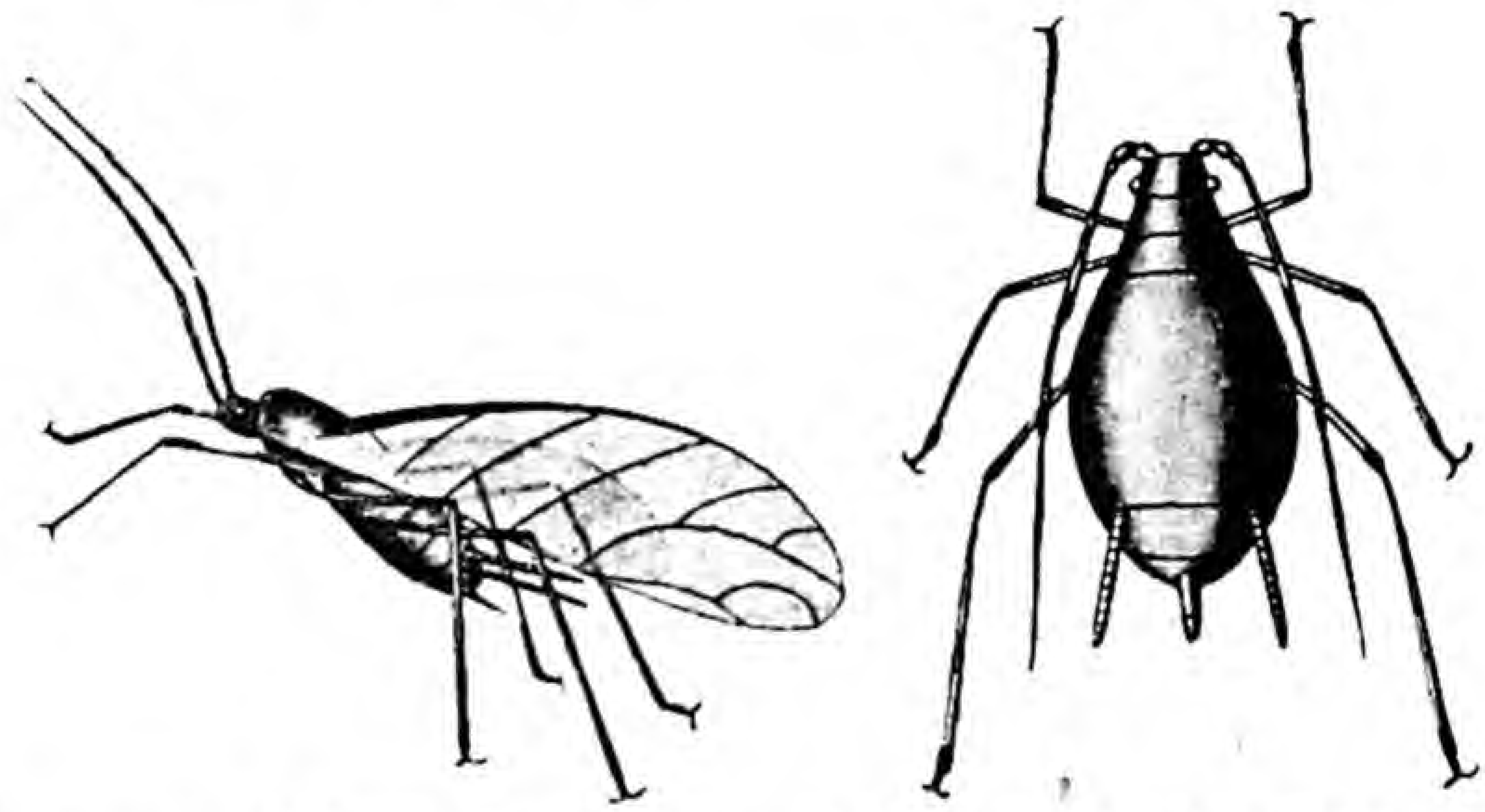


FIG. 449.—**Aphis rosæ** and larva. (From Cuvier's *Animal Kingdom.*

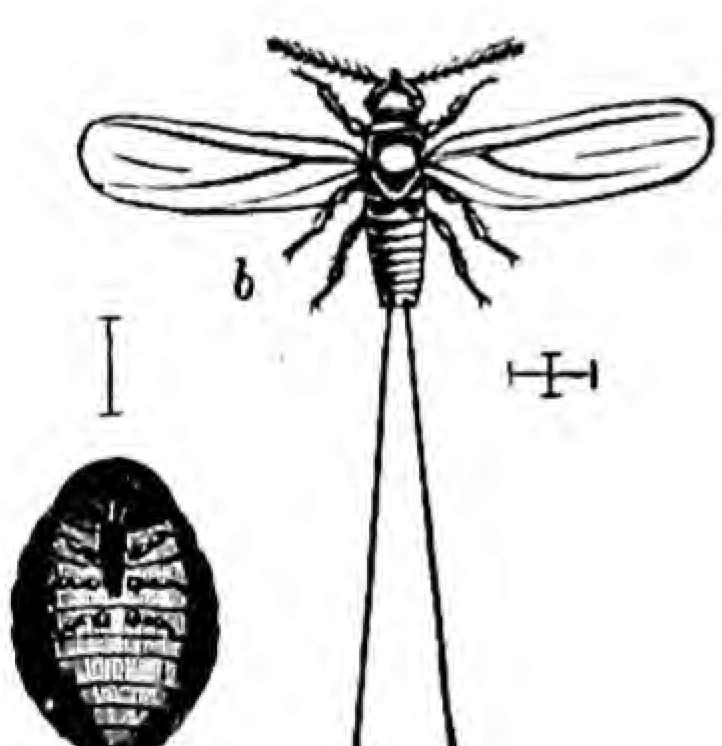


FIG. 450.—**Scale-insect (Coccus cacti).** *a*, female ; *b*, male. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Burmeister.)

FIG. 451.—One of the **Mallophaga** inhabiting the common fowl. (From the *Cambridge Natural History*, after Piaget.)

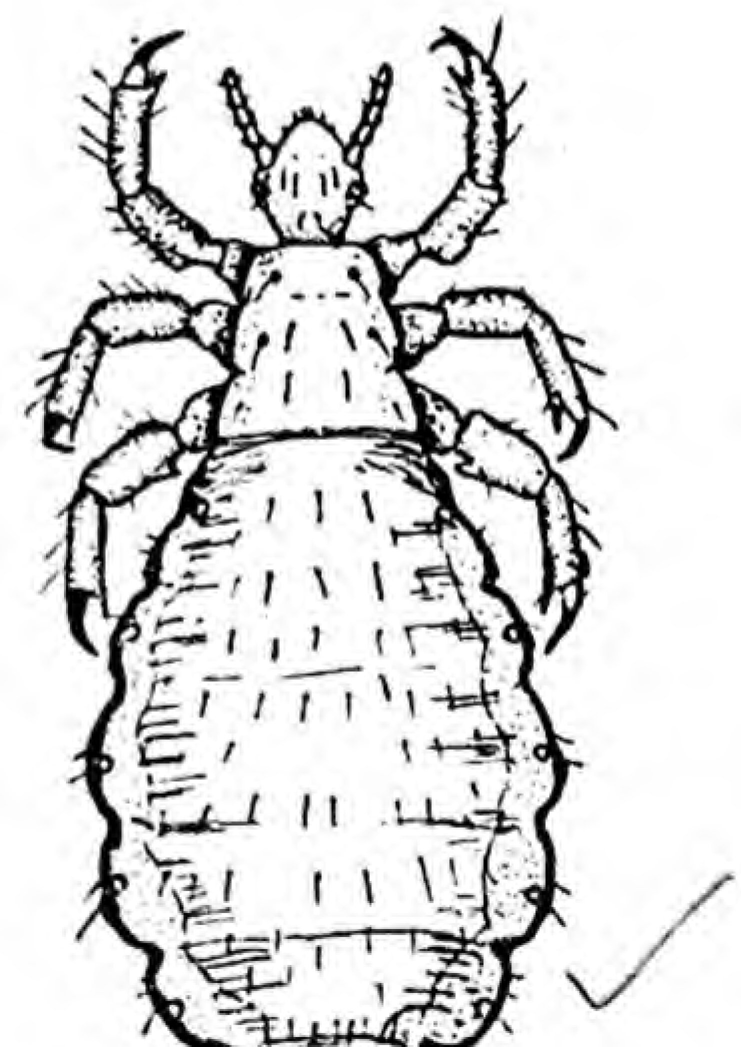


FIG. 452.—**Body Louse (Pediculus humanus)**, female. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

mostly on Birds and Mammals, living on horny fragments of feathers and hair (Fig. 451).

ORDER 11.—SIPHUNCULATA (ANOPLURA).

Ectoparasitic, secondarily wingless Exopterygota with piercing and sucking mouth-parts; metamorphosis absent.

This order comprises the *Sucking Lice* which are blood sucking parasites on Mammals (*Pediculus*, Fig. 452).

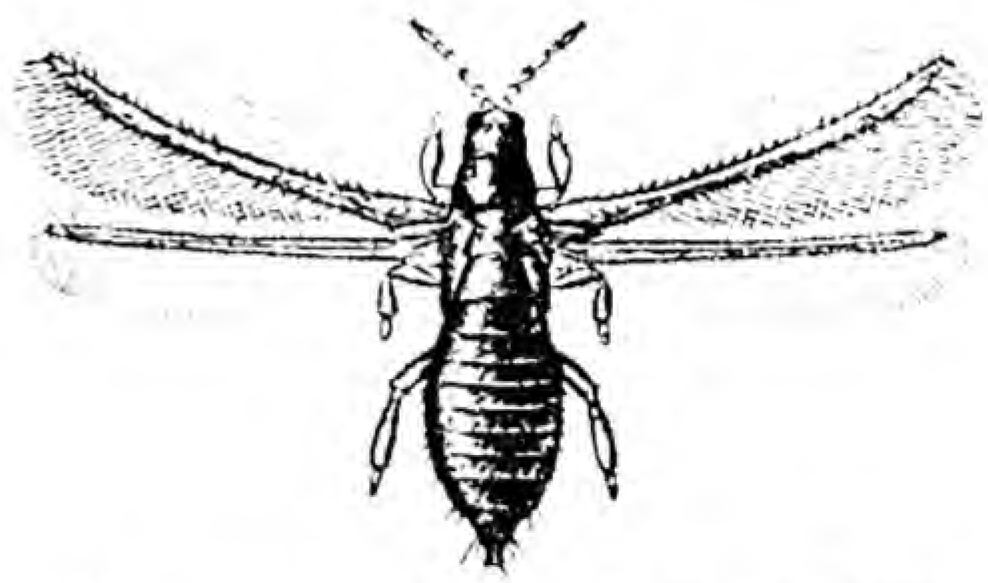


FIG. 453.—**Pear Thrips.** (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Foster and Jones.)

ORDER 12.—THYSANOPTERA.

Exopterygota, usually with two pairs of narrow, fringed wings; mouth-parts piercing; metamorphosis slight, including an incipient pupal instar.

This order comprises Insects usually of very small size, known as *Thrips* (Fig. 453).

DIVISION II.—ENDOPTERYGOTA (HOLOMETABOLA).

Pterygota which pass through a complete metamorphosis including a pupal stage; larvæ usually specialized; development of wings internal.

ORDER 13.—NEUROPTERA.

Endopterygota with two, generally similar pairs of wings; antennæ usually elongate; mouth-parts biting; larvæ with biting or sucking mouth-parts, usually with abdominal gills; pupæ not covered.

This order comprises the *Alder-flies*, *Lace-wings*, and *Ant-lions* (Fig. 454).

ORDER 14.—MECOPTERA.

Endopterygota with four elongated membranous wings (sometimes rudimentary or absent); biting mouth-parts borne at the end of a deflexed rostrum; carnivorous larvæ, caterpillar-like with three pairs of thoracic legs; abdominal feet present or absent; pupæ not covered.

This order includes the *Scorpion-flies* (*Panorpa*, Fig. 455).

ORDER 15.—TRICHOPTERA.

Moth-like Endopterygota with two pairs of membranous, hairy wings of unequal size; mouth-parts licking, mandibles vestigial or absent; aquatic larvæ, living in tubes built from foreign particles; pupation in tube.

This order comprises the *Caddis-flies* (Figs. 456, 457).

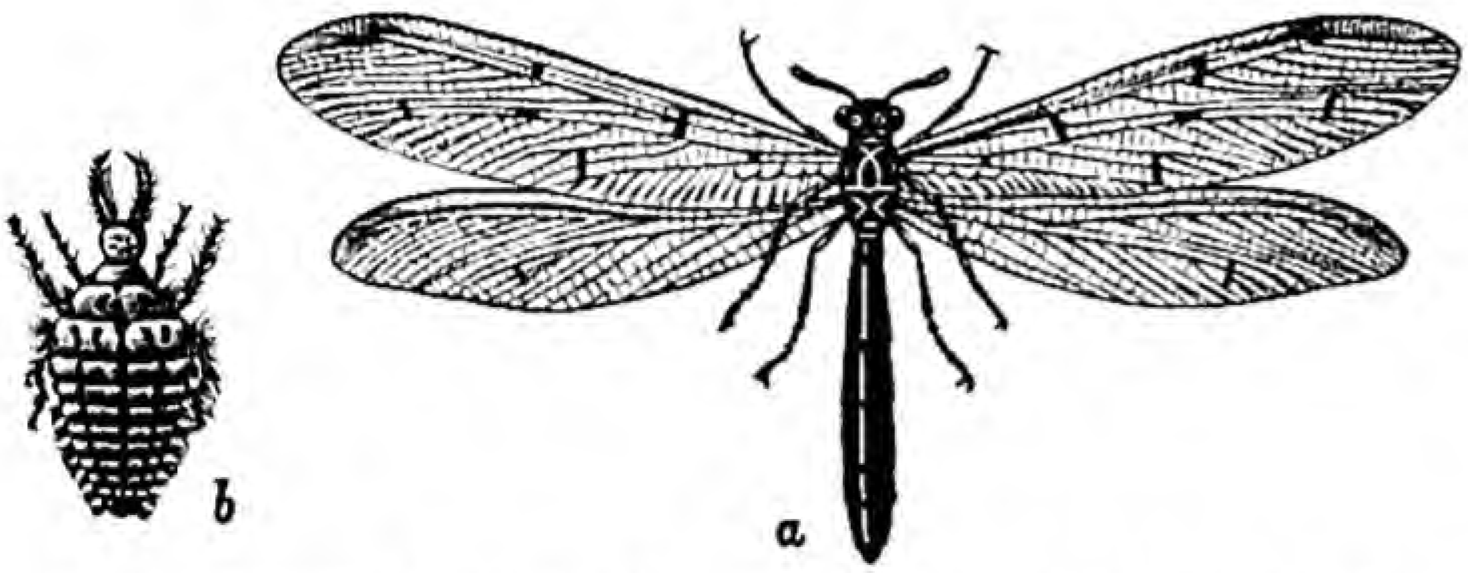


FIG. 454.—**Ant-lion (Myrmeleon formicarius)**, *b*, larva slightly enlarged. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer).)

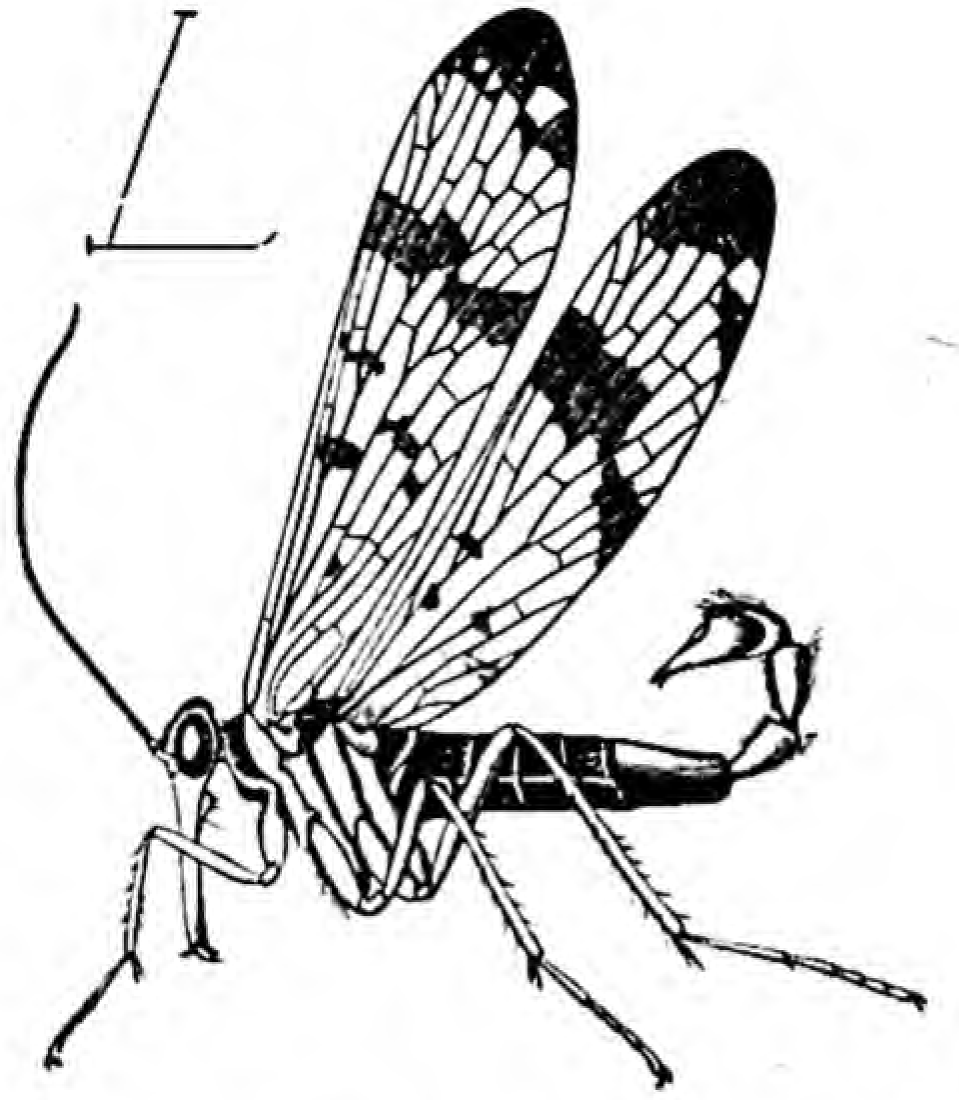


FIG. 455.—A Scorpion Fly (**Panorpa communis**), male. (After Sharp.)

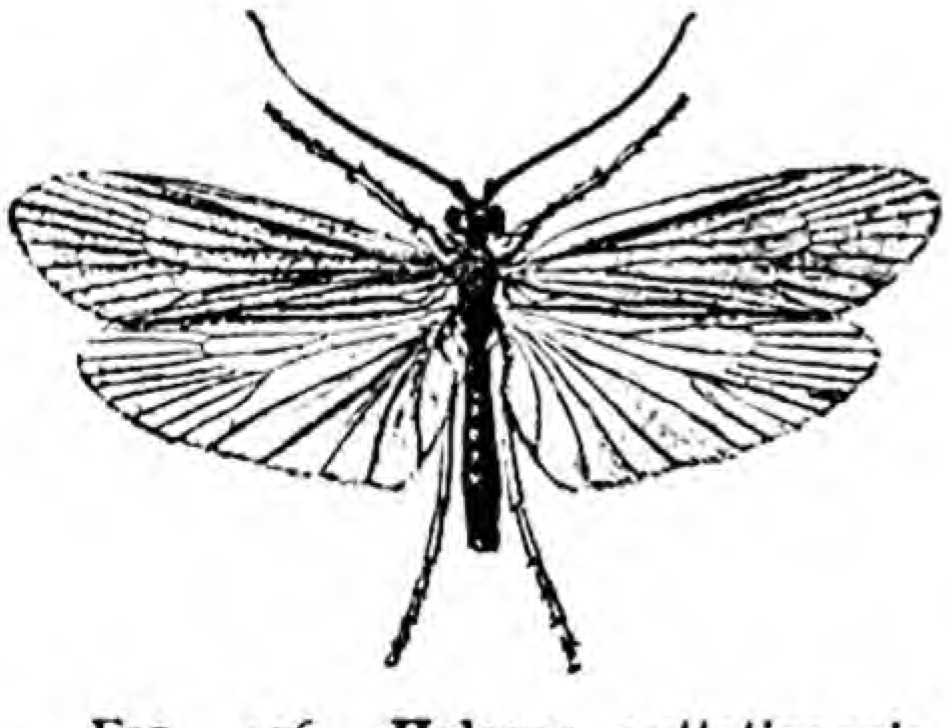


FIG. 456.—**Halesus guttatipennis.** (From Imms's *A General Textbook of Entomology*, Methuen & Co., Ltd.), after MacLachlan.)

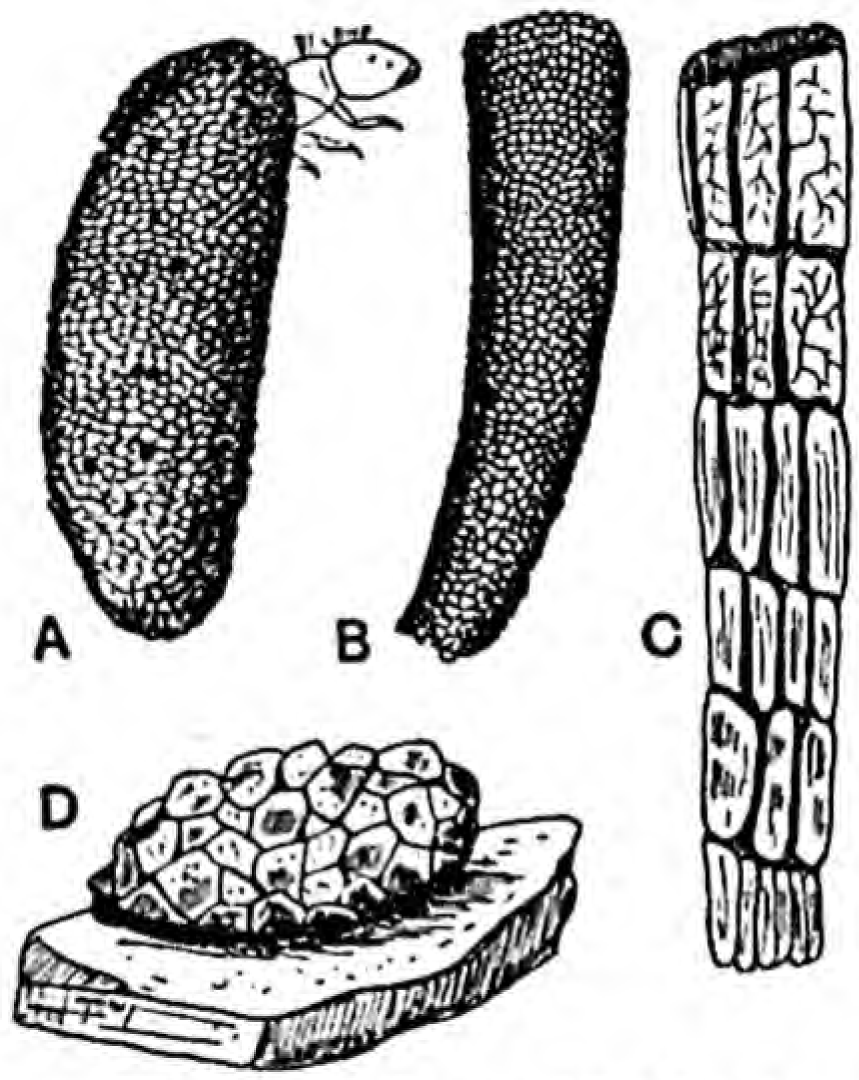


FIG. 457.—Cases of **Trichoptera.** *A*, *Hydroptila maclachlani*, case with larva; *B*, *Ondontocerum*, larval case; *C*, *Phryganea*, larval case; *D*, *Hydropsyche*, pupal shelter. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

ORDER 16.—LEPIDOPTERA.

Endopterygota with both pairs of wings well developed and covered with scales (modified hairs); the maxillæ are modified to form an elongated sucking tube, which can be rolled up spirally; the other parts of the mouth are rudi-

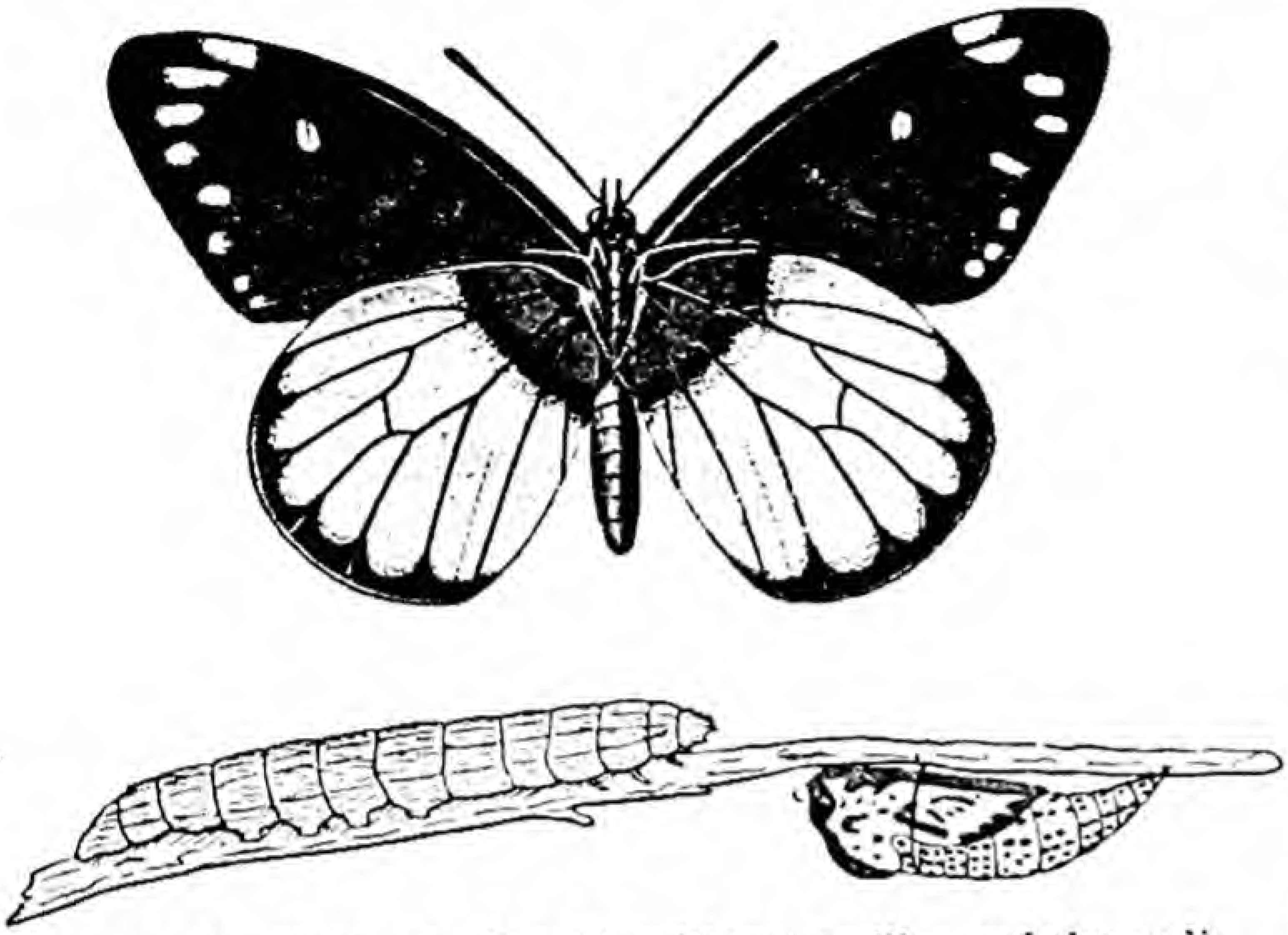


FIG. 458.—Butterfly (**Pieris**), with caterpillar and chrysalis stages. (After Guèrin and Percheron.)

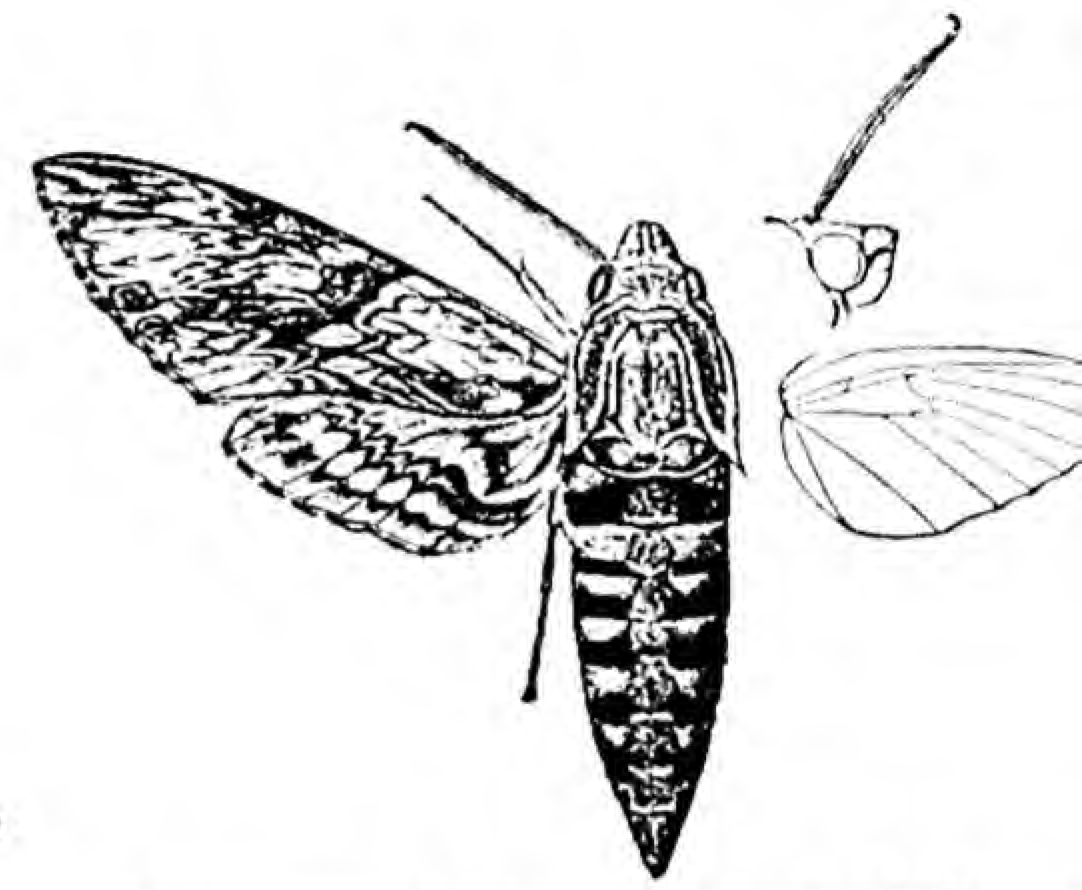


FIG. 459.—**Protoparce convolvuli**, m and venation of hind wing. (From Imn *A General Textbook of Entomology* (Meth & Co., Ltd.), after Hampson.)

mentary, with the exception of the labial palps; the prothorax is fused with the mesothorax; metamorphosis complete; larvæ typical caterpillars with three thoracic legs and frequently five pairs of abdominal feet; with biting mouth-parts; pupæ mostly more or less covered.

This order includes *Butterflies* (Fig. 458) and *Moths* (Fig. 459).

ORDER 17. COLEOPTERA.

Endopterygota in which the arterior pair of wings take the form of hard horny wing-cases, or *elytra*, which, when at rest, are folded up along the back and cover over the folded-up membranous posterior wings; the prothorax is movable on the other segments; the jaws are fully developed, and adapted for biting and chewing; metamorphosis complete; larvæ *either* primitive with well developed thoracic legs, and cerci, with biting mouth-parts, *or* caterpillar-like, less active; sometimes larvæ are legless and maggot-like; pupæ not covered.

FIG. 460.—**Melolontha vulgaris.** *1.* imago; *1.a.* larva. (From Ministry of Agriculture and Fisheries, Leaflet No. 25, by permission of H.M.S.O.)

This order includes the true Beetles (Fig. 460).

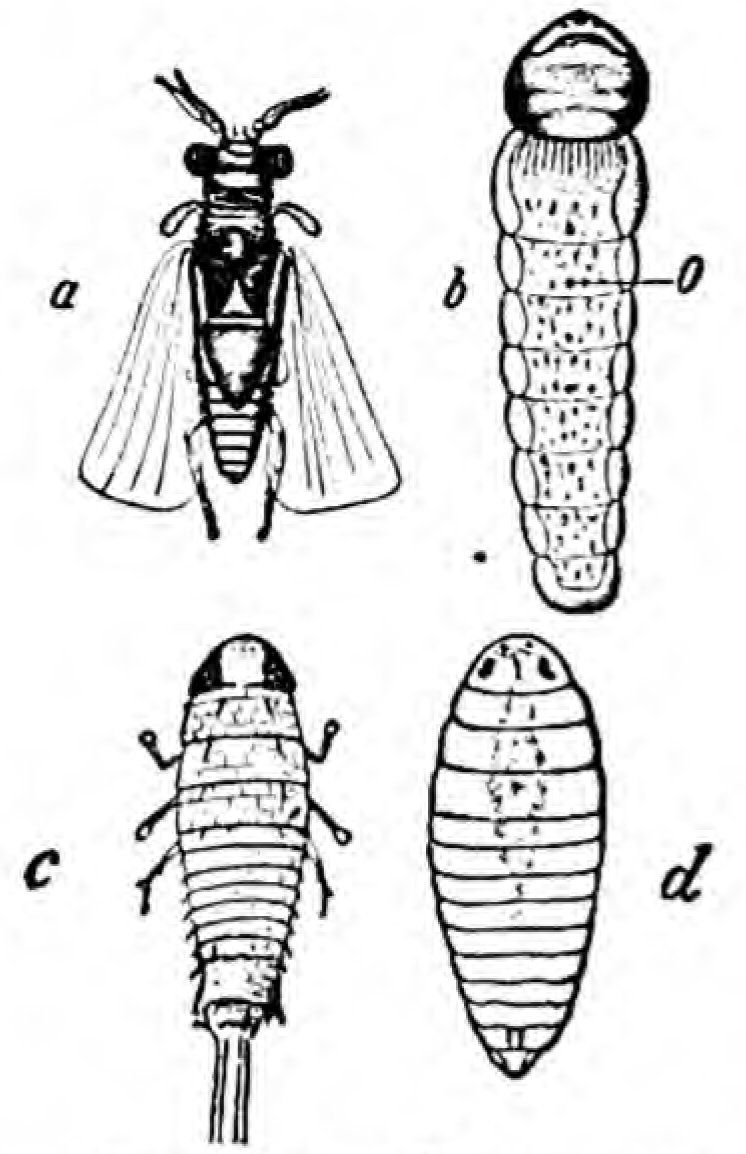


FIG. 461.—**Xenos vesparum.** *a*, male; *b*, female; *c*, free larva; *d*, legless parasitic larva; *o*, genital pore. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Nassonow.)

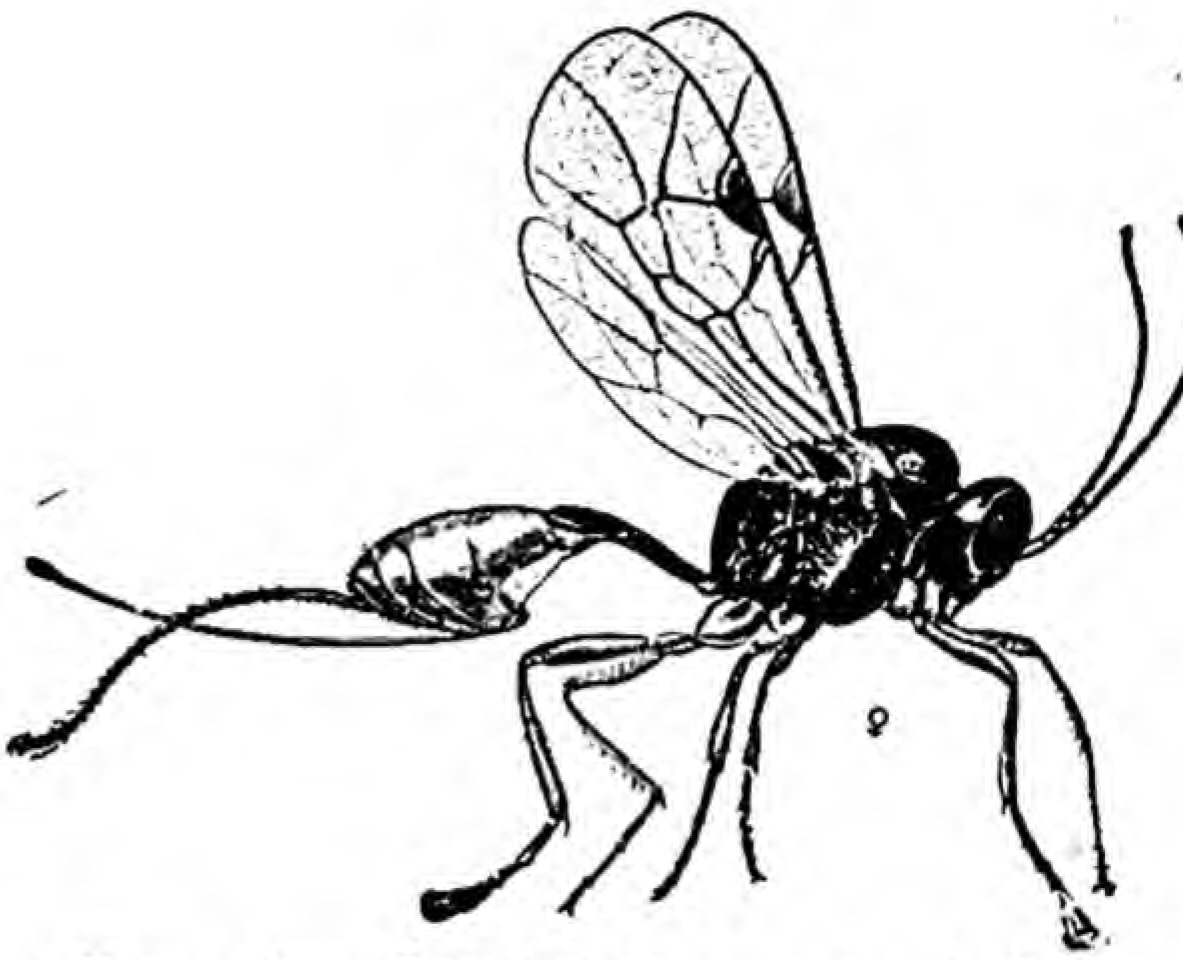


FIG. 462.—**Thersilochus conotracheli,** female. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Cushman.)

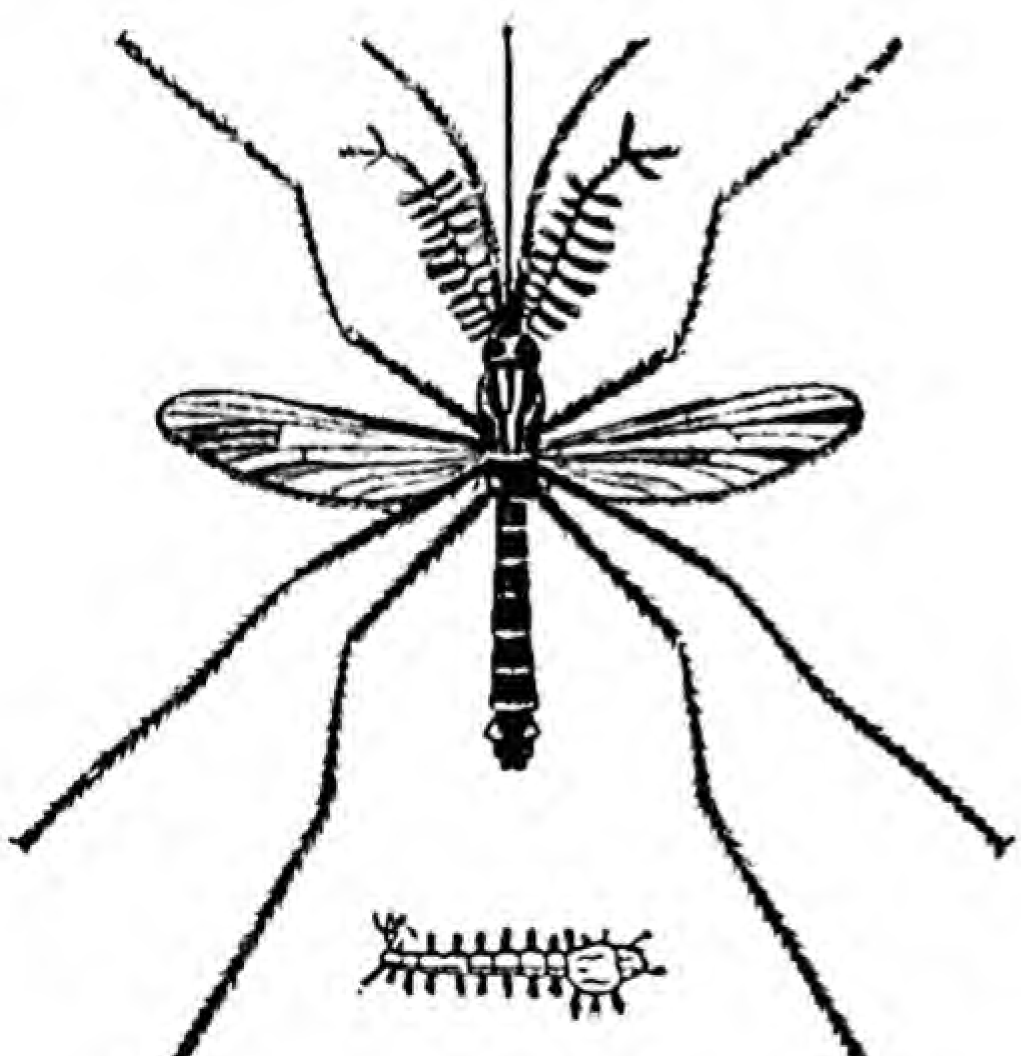


FIG. 463.—**Culex** (mosquito) and larva. (After Guèrin and Percheron.)

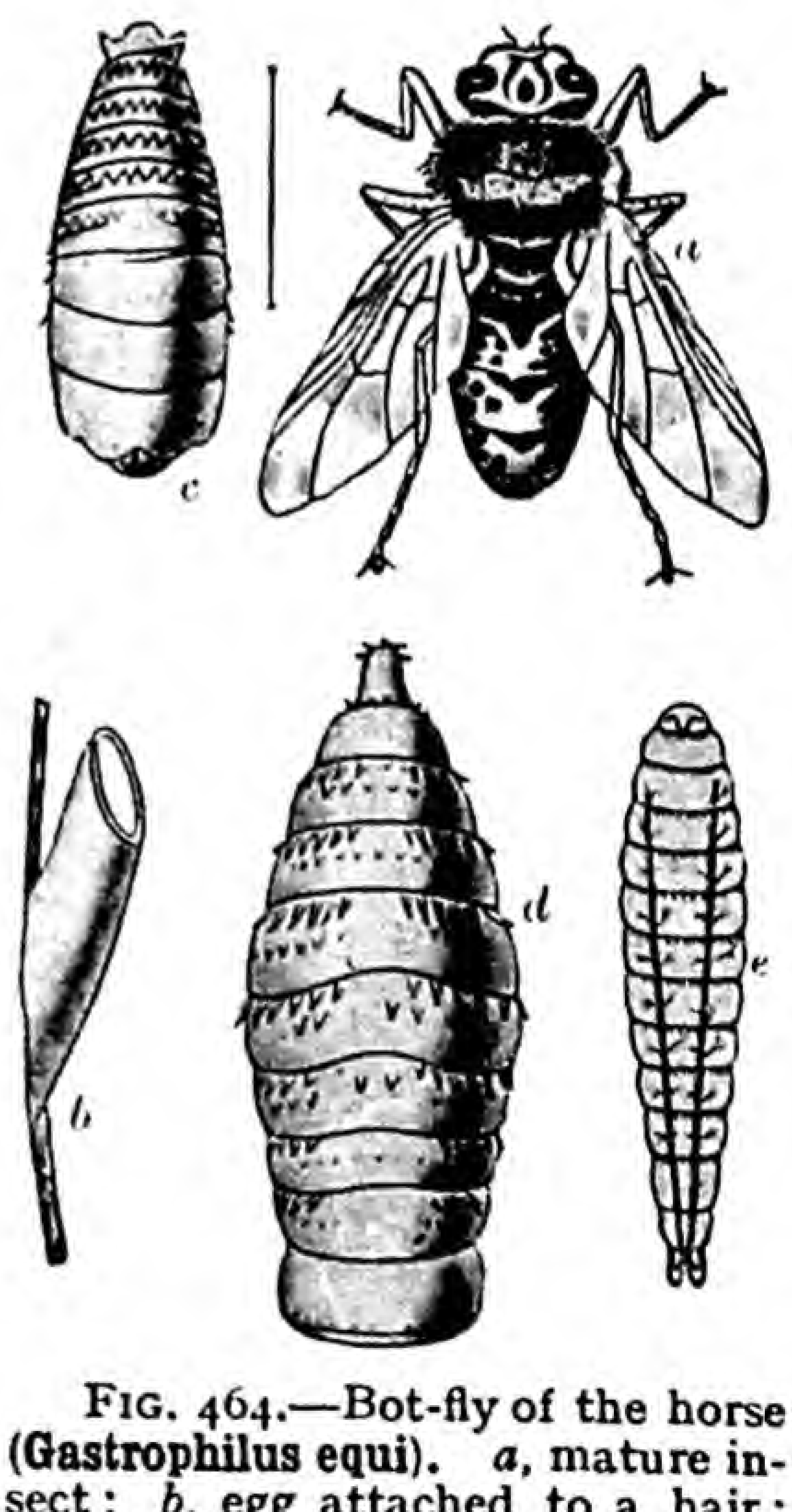


FIG. 464.—Bot-fly of the horse **(Gastrophilus equi).** *a*, mature insect; *b*, egg attached to a hair; *c*, *d*, and *e*, stages in the larval development. (After Brehm.)

ORDER 18.—STREPSIPTERA.

Small endoparasitic Endopterygota, males winged and free-living; endoparasitic females larviform; anterior wings of male modified into halteres; metamorphosis complete.

Examples: *Stylops* and *Xenos* (Fig. 461), parasitic in Hymenoptera.

ORDER 19. HYMENOPTERA.

Endopterygota in which both pairs of wings are present and membranous; mouth-parts adapted for biting and licking; the prothorax is united with the

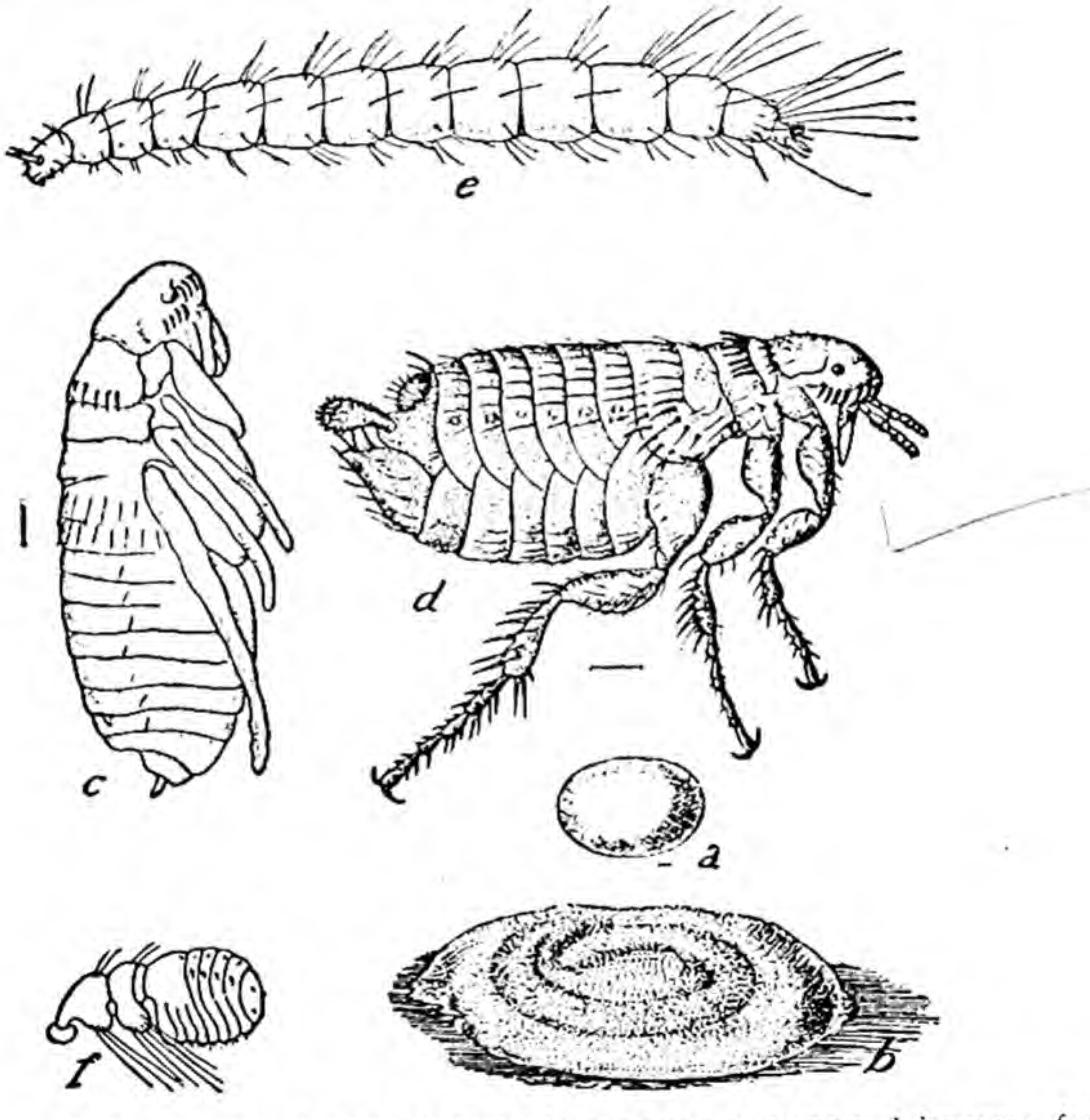


FIG. 465.—**Ctenocephalus canis.** *a*, egg; *b*, larva in cocoon; *c*, pupa; *d*, imago; *f*, antenna of imago; *e*, *Ceratophyllus fasciatus*, larva. (From Imms's *A Textbook of Entomology* (Methuen & Co., Ltd.), all except *e* after Howard.)

other segments of the thorax; metamorphosis complete; larvæ mostly legless, grub-like; pupæ generally protected by a cocoon.

Included in this order are *Bees* (Fig. 486), *Wasps*, *Ants* (Fig. 487), *Gall-flies*, and *Ichneumons* (Fig. 462).

ORDER 20.—DIPTERA.

Endopterygota provided with a single pair of transparent wings, repre-

senting the anterior pair of other orders; hind pair of wings modified into so-called halteres; mouth-parts adapted for piercing and sucking; the prothorax is fused with the other segments of the thorax; metamorphosis complete; larvæ legless, often grub-like; pupæ free or covered.

This order includes *Gnats* and *Mosquitoes* (Fig. 463), House-flies and Blow-flies, Bot-flies (Fig. 464) and " Daddy-long-legs."

ORDER 21.—APHANIPTERA.

Small, secondarily wingless Endopterygota with piercing and sucking mouth-parts; living ectoparasitically on warm blooded animals; metamorphosis complete; larvæ legless; pupæ in cocoon.

This order includes the *Fleas* (Fig. 465).

3. GENERAL ORGANIZATION.

The **exoskeleton** of the Insecta (Fig. 466) consists of a chitinous cuticle (*cut.*), which varies in hardness and thickness in different Insects and in different parts of the body of the same Insect, but is very rarely calcified. Frequently it presents hexagonal markings; sometimes it is perforated by numerous pores; sometimes it is covered with thin scales; in many cases it is developed into *tactile bristles* (*t. b.*) or *setæ*, which may be scattered over the body, or may be located mainly on certain of the appendages—the antennæ, the maxillary and labial palpi, and the tarsi of the legs. In some, *glands* are present in the integument—odoriferous, and wax-forming glands; poison glands are present in connection with an abdominal sting in certain Insects; spinning glands, forming a silky material, are confined to the larvæ.

The **head** presents but few indications of segmentation, but the history of its development indicates that it may be looked upon as composed of a pre-antennary and five further segments, intimately united together. It varies a good deal in shape, but always presents the regions that have already been described in the case of the Cockroach. Of these the *epicranium* is the most extensive; the *clypeus*, situated in front of it, supports the labrum; the *genæ* are situated laterally, and a median piece, the *gula*, occupies the middle of the ventral surface. Sometimes the head is sunk within the anterior part of the thorax; sometimes it is free from the latter; and there may be, as in the Cockroach, a short narrow region or *neck*, covered with soft skin, supported only by isolated *cervical sclerites*, on the ventral aspect.

The three segments of the **thorax**—*pro-*, *meso-*, and *meta-thorax*—are usually firmly united together; but in some Insects the prothorax is movable upon the other segments: it is usually the smallest of the three segments. In each the exoskeleton consists of *dorsal* or *tergal* and *ventral* or *sternal* elements, some-

times separate from one another laterally, sometimes united together in such a way as to form complete rings round the segments. Laterally projecting processes or *pleura* are sometimes developed.

The **abdomen** contains up to eleven segments, enclosed in tergal and sternal shields. In some Insects the first abdominal segment is united with the thorax so as to appear to belong to the latter region.

The **appendages of the head** are four pairs, as in the Cockroach; but a considerable variation is observable in the different orders, especially as regards the jaws. In certain of the Apterygota an additional pair—the so-called superlinguæ (Fig. 418, 4)—occur between the mandibles and first maxillæ. In a few eyes are absent. Most have large compound or faceted eyes, and many have simple eyes or ocelli as well; in a few groups the latter are alone present. The antennæ vary in shape in different groups and sometimes even in the sexes of the same species. They may be tapering, moniliform, club-shaped, pectinate, or plume-like. In addition to functioning as tactile appendages they bear olfactory sensillæ, vibration receptors and proprioceptive organs. The mandibles are always one-jointed, and differ from those of the Crustacea in never being provided with a palp. An arrangement of the mouth-parts adapted for biting or chewing has already been described in the case of the Cockroach (Figs. 418, 467): this type is characteristic of the order Orthoptera, to which the Cockroach belongs, and a very similar type characterizes the Coleoptera. In the Hymenoptera (Fig. 468) the mouth-parts are adapted both for biting and for licking; the mandibles (*Md.*) and maxillæ ($Mx._1$) are sharp and lancet-like; the middle part of the labium is produced into a long median tongue (*glossa*, *Gl.*) at the sides of which are a pair of accessory tongues or *paraglossæ* (*Pgl.*). In the Hemiptera (Fig. 471) there is a proboscis formed from the labium ($Mx._2$) and enclosing the stylet-like mandibles and maxillæ. In the Diptera (Fig. 470) the mandibles, usually not developed in the males, are biting or piercing organs, while the basal parts of the labium form a proboscis ($Mx._2$) enclosing a spine or seta (*Hy.*)—which is a process from the *hypopharynx*—and sometimes stylet-like maxillæ ($Mx._1$). In the Lepidoptera (Fig. 469) the mandibles are reduced in the adult, and the maxillæ ($Mx._1$) are developed into elongated half-tubes, which when applied together form a complete tube capable of being coiled up in a spiral manner under the head.

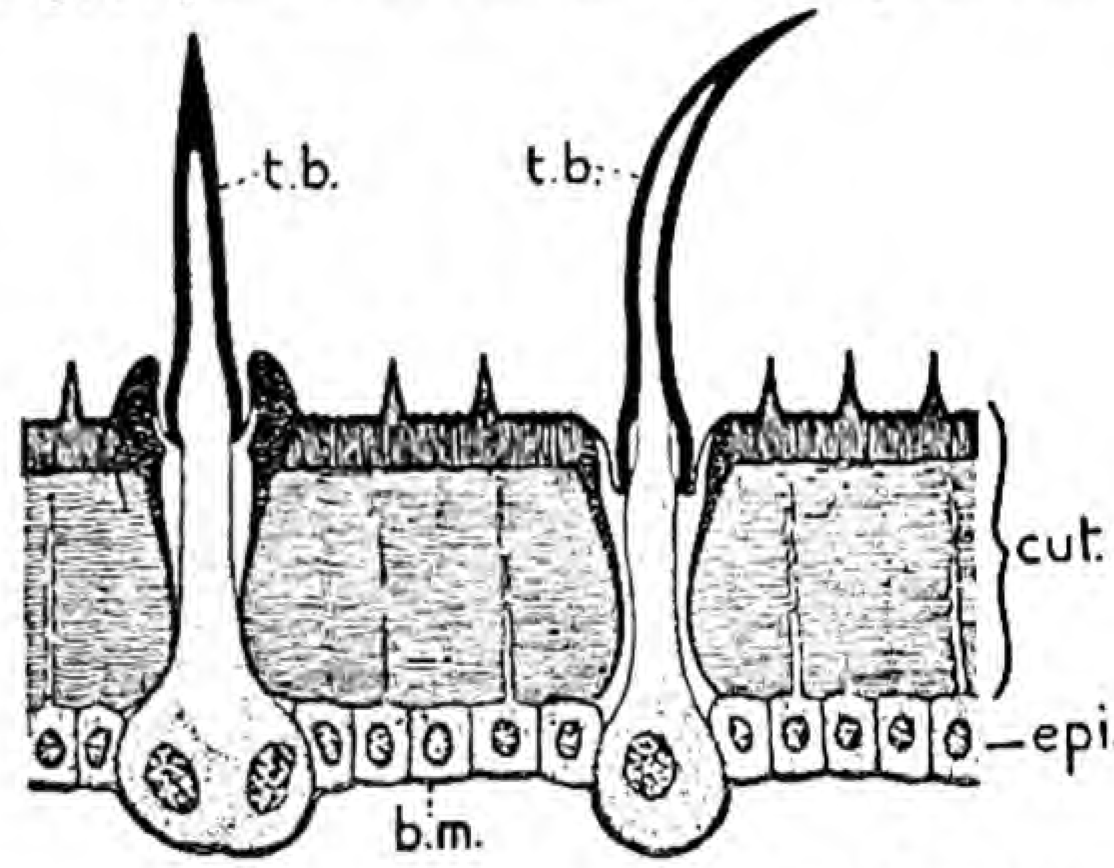


FIG. 466.—**Section through the integument of an Insect.** *b. m.* basement membrane; *cut.* layers of the cuticle; *epi.* epidermis; *t. b.* tactile bristles. (From Weber's *Lehrbuch der Entomologie* (Gustav Fischer, Jena).)

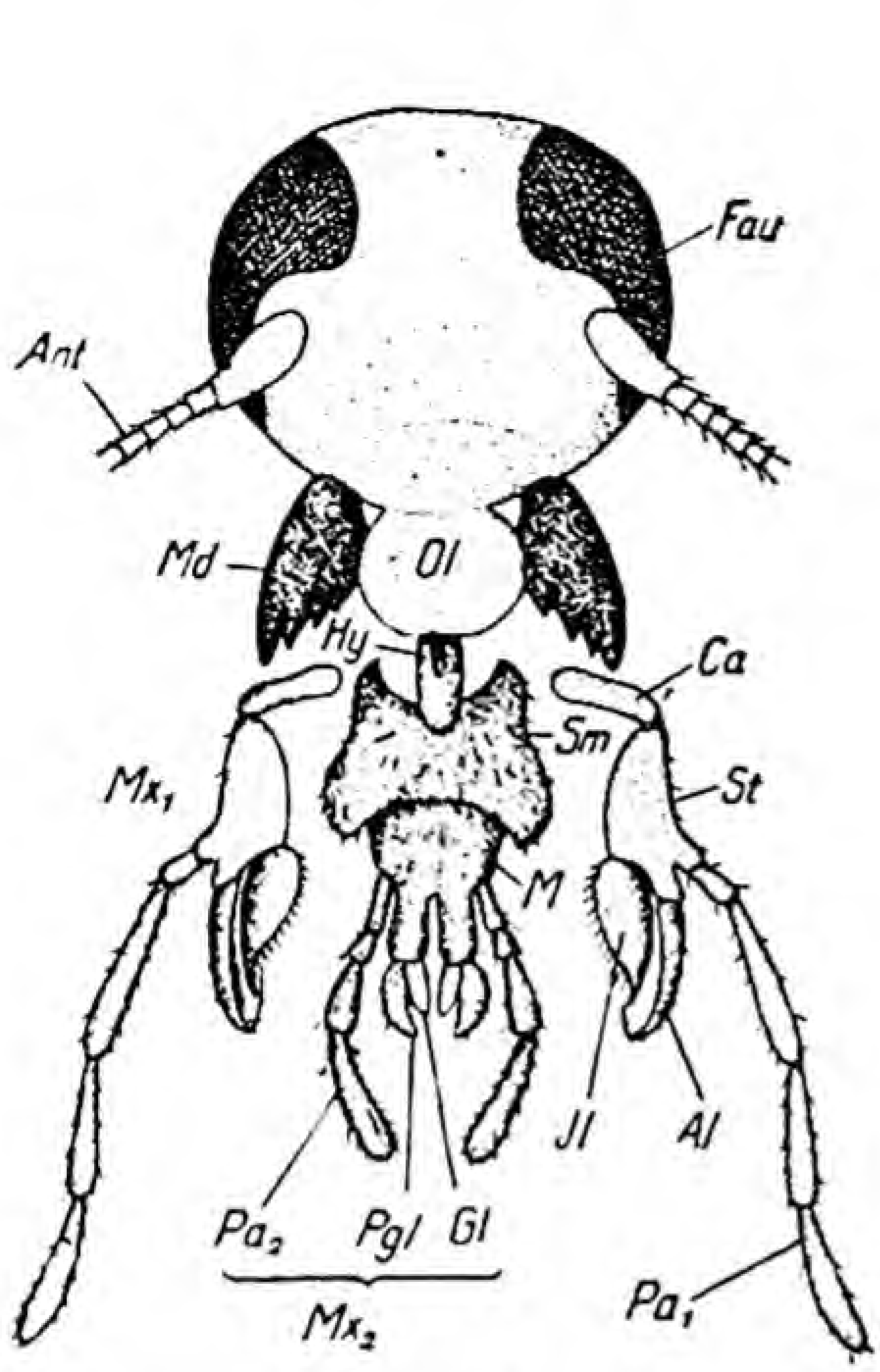


FIG. 467.

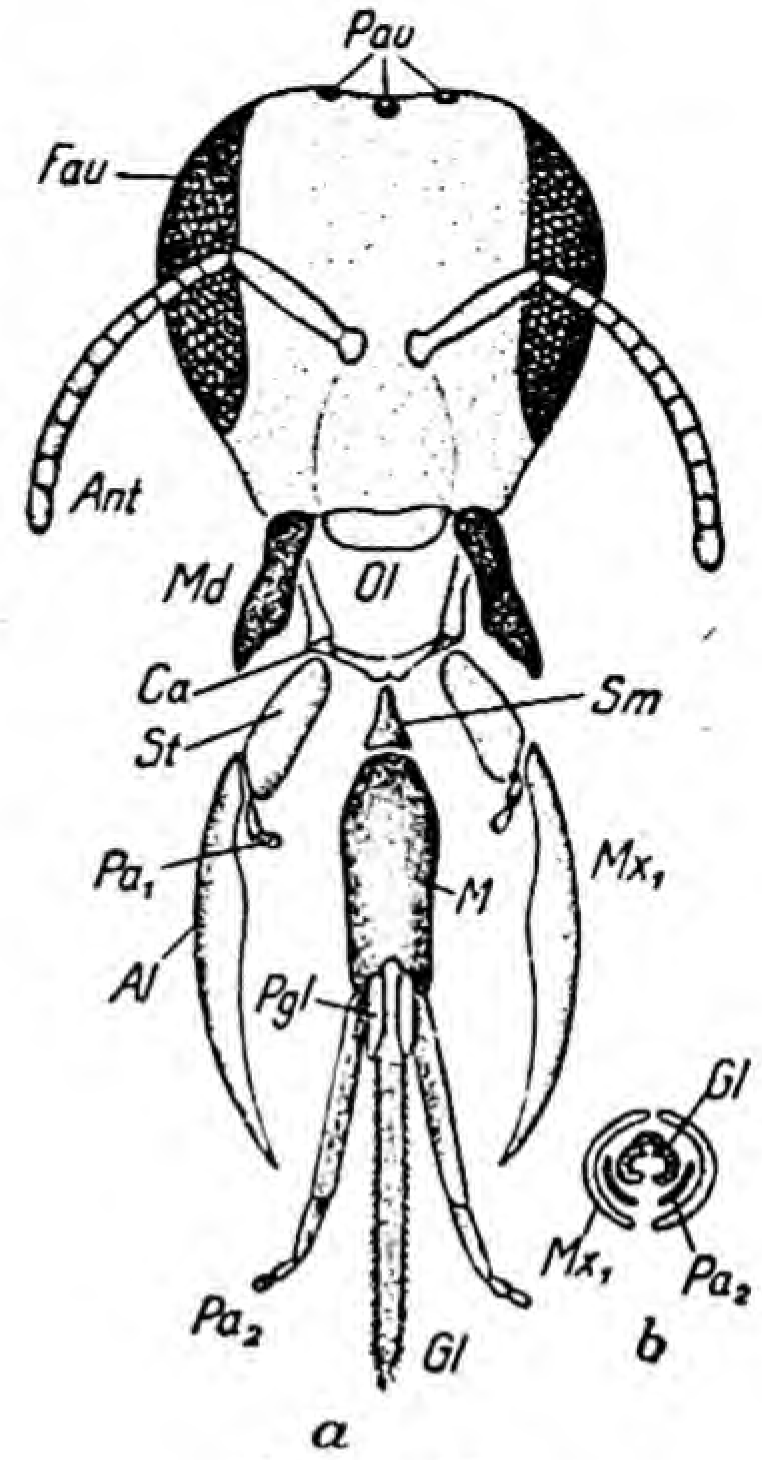


FIG. 468.

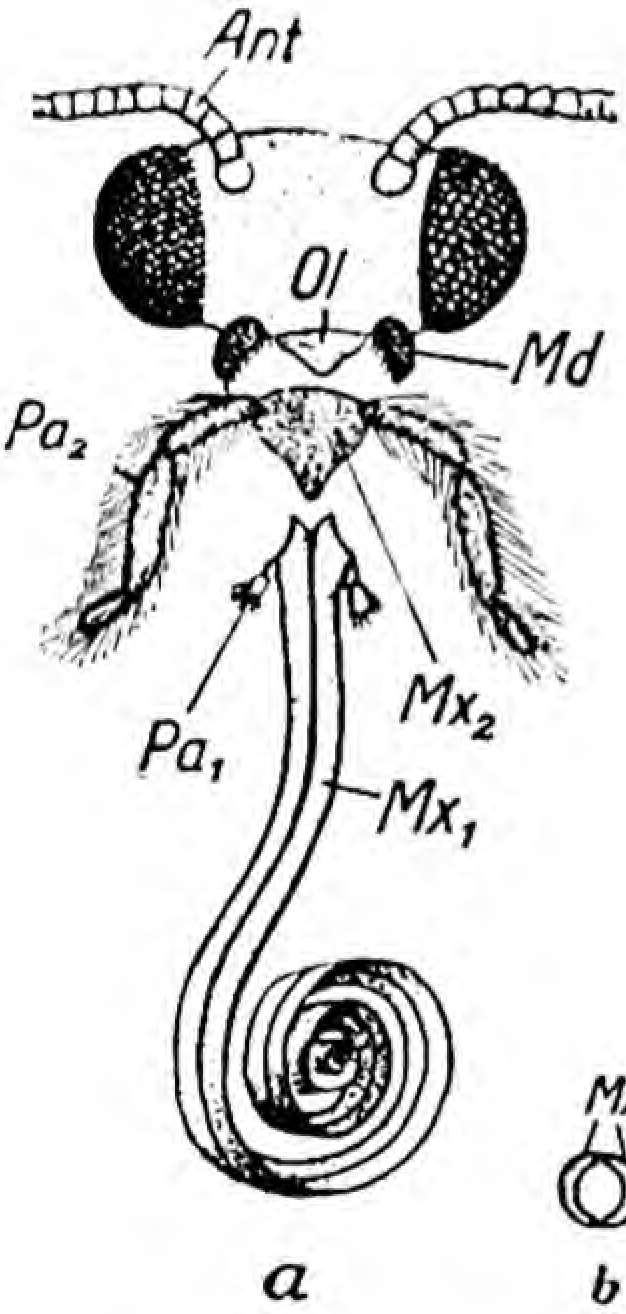


FIG. 469.

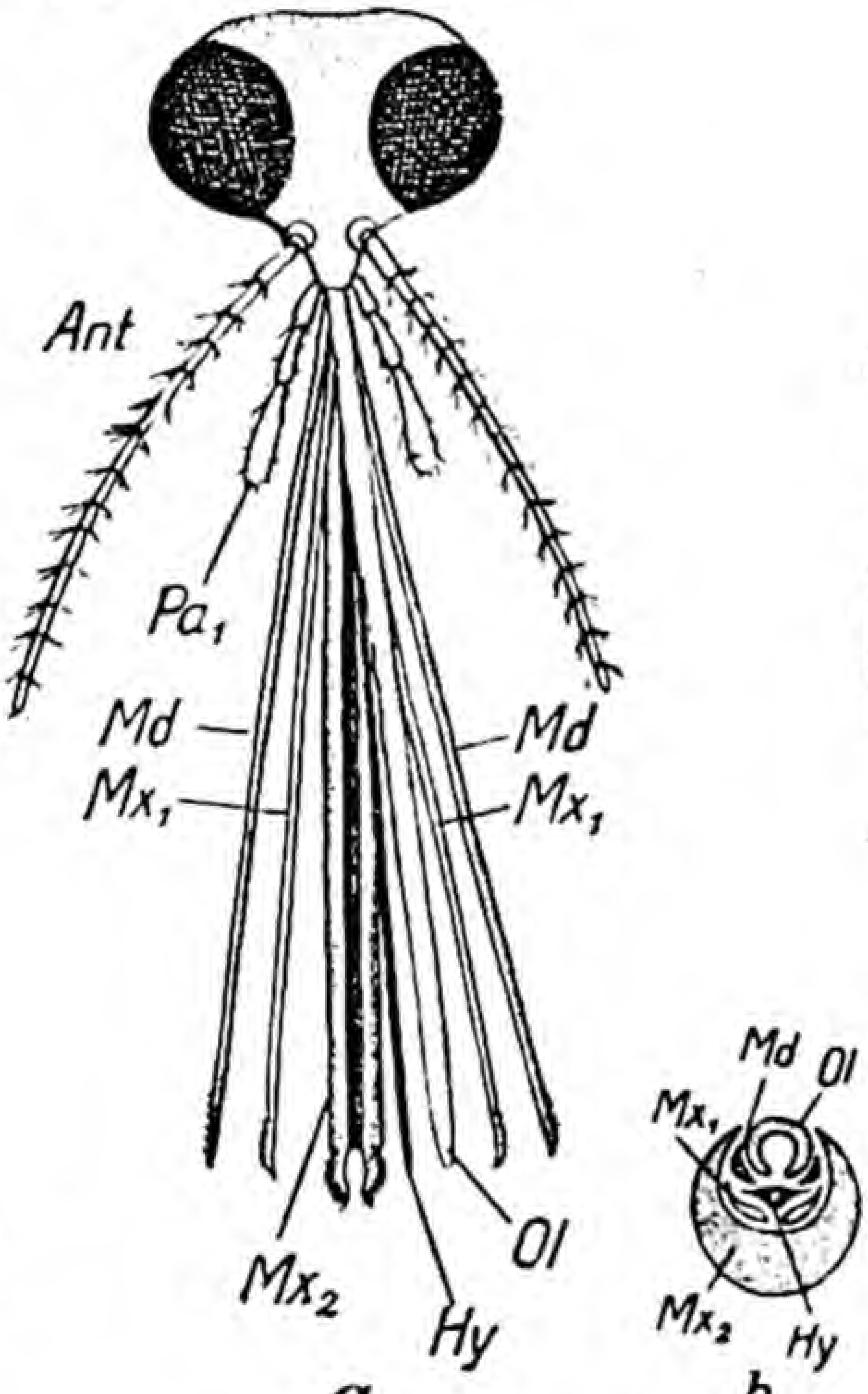


FIG. 470.

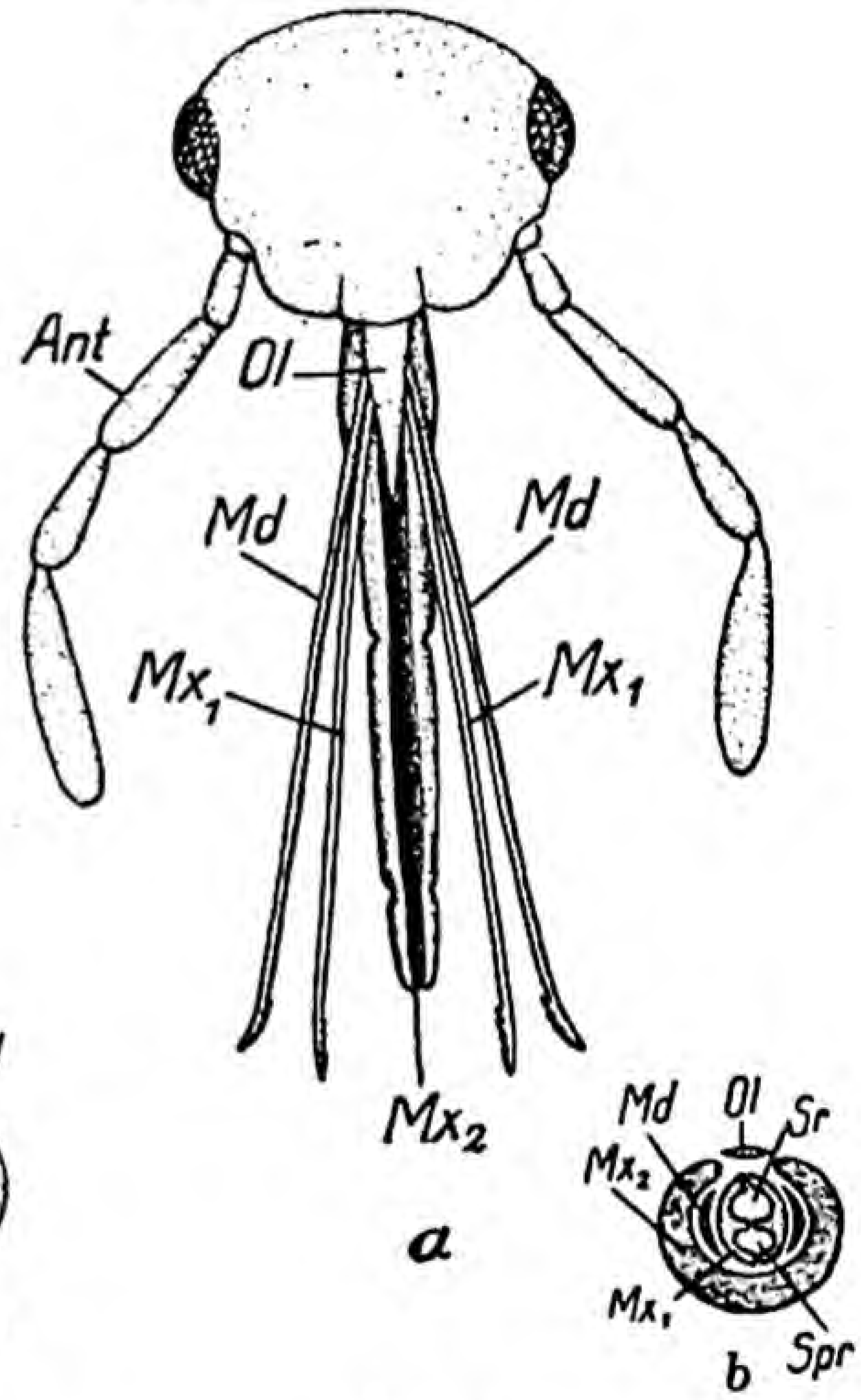


FIG. 471.

FIGS. 467–471.—Comparative diagrams of the **Mouth-parts of various Insects.** 467, *Orthoptera*; 468, *Hymenoptera*; 469, *Lepidoptera*; 470, *Diptera*; 471, *Hemiptera*. *Al.* galea; *Ant.* antenna; *Ca.* cardo; *Fau.* compound eye; *Gl.* glossa; *Hy.* hypopharynx; *Il.* lacinia; *M.* mentum; *Md.* mandible; *Mx.*$_1$ first maxillæ; Mx.$_2$ second maxillæ; *Ol.* labrum; *Pa.*$_1$ and *Pa.*$_2$ maxillary palps; *Pau.* ocelli; *Pgl.* paraglossa; *Sm.* submentum; *Spr.* salivary tube; *Sr.* sucking tube; *St.* stipes. (From Kühn's *Grundriss der Allgemeinen Zoologie* (George Thieme, Leipzig).)

Appendages of the thorax.—Each of the segments of the thorax bears a pair of five-jointed legs; the terminal section or tarsus being made up of a number of short segments, usually five, and ending in a pair of claws, often with an adhesive pad or sucking disc between them, or in a single claw. In accordance with variations in the uses to which they are put, considerable differences are observable in the form of the legs in different groups of Insects. In most they are adapted for walking, and are long and slender; in some they are expanded to enable them to act as swimming paddles; in some the first pair are prehensile, and develop a sub-chelate extremity; in others, again, the legs, or the first pair of them, are stout and adapted for burrowing. In addition to the legs the meso- and metathorax may each bear a pair of *wings*. The wings are thin transparent expansions of the integument of the body, supported by a system of branching ribs or *nervures* consisting of chitinous material with branches of the tracheæ, nerves, and tubular diverticula of the body-cavity. In most Lepidoptera the wings are opaque, owing to their being covered with numerous overlapping microscopic scales, to which the various colours of the wings are due. In some Insects—*e.g.*, Beetles and Orthoptera—the posterior wings alone are delicate and membranous, the anterior pair being converted into hard or tough cases—the *elytra*—which when folded up cover over and protect the delicate posterior wings. In some Beetles the elytra are permanently united together along the back of the Insect. In some Insects (Bugs) the anterior wings are chitinous at the bases only. In the Diptera the anterior wings alone are developed, the posterior being represented by vestiges—the *halteres* or balancers. In the Strepsiptera, or Bee-parasites on the other hand, it is the anterior pair that are vestigial. In some Insects (Spring-tails, Lice, Fleas) wings are entirely absent in all stages. In others again they are present in one sex—usually the male—and absent or vestigial in the other. In the Apterygota there is no vestige whatever of wings at any stage, and this, taken in connection with the simplicity of the structure in other respects, seems to indicate that in these Insects we have to do with the descendants of a primitive group in which wings had not yet become developed.

The segments of the **abdomen** are mostly devoid of paired appendages in the adult condition (except in the Thysanura), though vestiges of them may be present in the young at an early stage. Each segment is enclosed in dorsal *tergal* and ventral *sternal* plates, which usually remain separate laterally, but may be united. At the extremity of the abdomen there are frequently appendages which are perhaps of the nature of limbs, having the function of stings, ovipositors, and genital processes.

Hæmocœle.—The cavity intervening in an Insect between the body-wall and the various internal organs does not correspond, as already explained (p. 447), to the cœlome of other groups, but is found, when we study its mode of development, to be a *hæmocœle*—an extended part of the blood-vascular

system. The cœlome is apparently represented only by the lumen of the reproductive organs.

A **fat-body** is always present, either in the larval condition or throughout life. It consists of a mass of polygonal cells bounding the hæmocœle externally. When young the cells are nucleated and possess a protoplasmic body. At a later stage a fluid loaded with minute granules takes the place of the protoplasm, and sometimes crystals of salts of uric acid are also stored. These crystals afterwards become absorbed; their appearance and subsequent absorption would seem to point to the probability that the fat-body is concerned in separating out nitrogenous waste matters, which subsequently reach the exterior through the Malpighian tubes. Its chief function is to serve as a reserve-store of nutrient material.

Digestive system.—Some Insects do not feed in the adult condition, and when this is the case the mouth may be absent, as, for example, is the case in the May-flies (*Ephemeridæ*). When a mouth is developed, as it is in the vast majority of Insects, it is situated on the lower aspect of the head, bounded in front by the labrum, and behind by the labium. It leads into the buccal cavity or pharynx, into which open the ducts of a pair of *salivary glands*, each of which often has associated with it a thin-walled sac or *salivary receptable.* Also in the neighbourhood of the mouth in such larval Insects as spin a cocoon, the ducts of a pair of *spinning glands* open. A projection of the roof of the mouth-cavity (*epipharynx*) is present in some Insects; in others it is replaced by a projection from the floor, the *hypopharynx* or *lingua.*

The alimentary canal is nearly always considerably longer than the body; it is longer in vegetable-feeding than in carnivorous forms. The pharynx leads into a long, narrow passage—the *œsophagus* (Figs. 472 and 473 *œ.*)—which dilates behind into a *crop* (*in, hm*) for the storage of food. The place of this in sucking Insects is taken by a stalked sac, which functions as a food reservoir. The essential processes of digestion are carried on in an elongated chamber with glandular walls—the *stomach* (*cd, cm*)—which may be divided into several parts. Sometimes between the crop and stomach is intercalated a muscular-walled chamber, frequently containing chitinous teeth, the *proventriculus* or *gizzard* (*pv*). Appended to the stomach at its anterior end are, in many Insects, a varying number of tubular blind pouches, the *hepatic cæca.* At its junction with the small intestine there open a number (from 2 to over 100) of narrow tubular appendages, the *Malpighian tubes* (*vm*), which are the organs of renal excretion. In the cases in which the development of the alimentary canal has been traced, it has been found that the Malpighian tubes mark the point where the mesenteron passes into the proctodæum, and it is assumed that this holds good generally. In some insects, the Malpighian tubes open into a paired or unpaired sac—the *urinary bladder.* The intestine is usually elongated, and its posterior portion (*ed.*) is dilated to form a wide *rectum* (*r.*), which opens

on the exterior by an anal aperture situated on the ventral side of the last segment of the abdomen. *Anal glands* (*ad.*), producing an odoriferous secretion, often open into the rectum.

The **tracheal system** (Fig. 473) communicates with the exterior through a number of apertures—the *stigmata* (*st*)—which vary in the details of their arrangement in the different orders. They are always protected against the

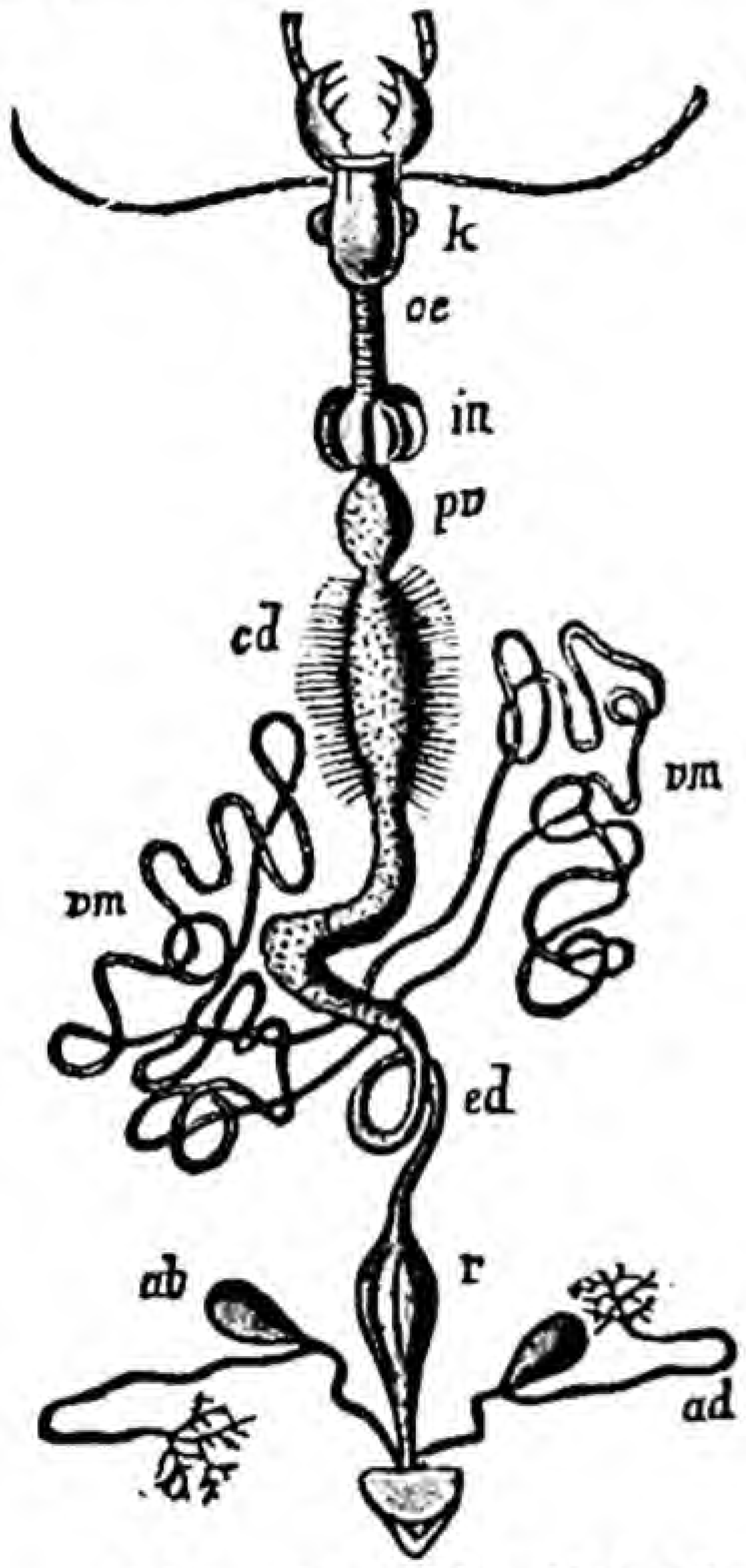


FIG. 472.—Digestive apparatus of a Beetle (**Carabus auratus**). *ad*, anal glands; *ab*, their muscular appendages; *cd*, stomach; *ed*, hind gut; *in*, crop; *k*, head with mouth-parts; *œ*. œsophagus; *pv*. proventriculus; *vm*. Malpighian tubes. (From Lang, after Dufour.)

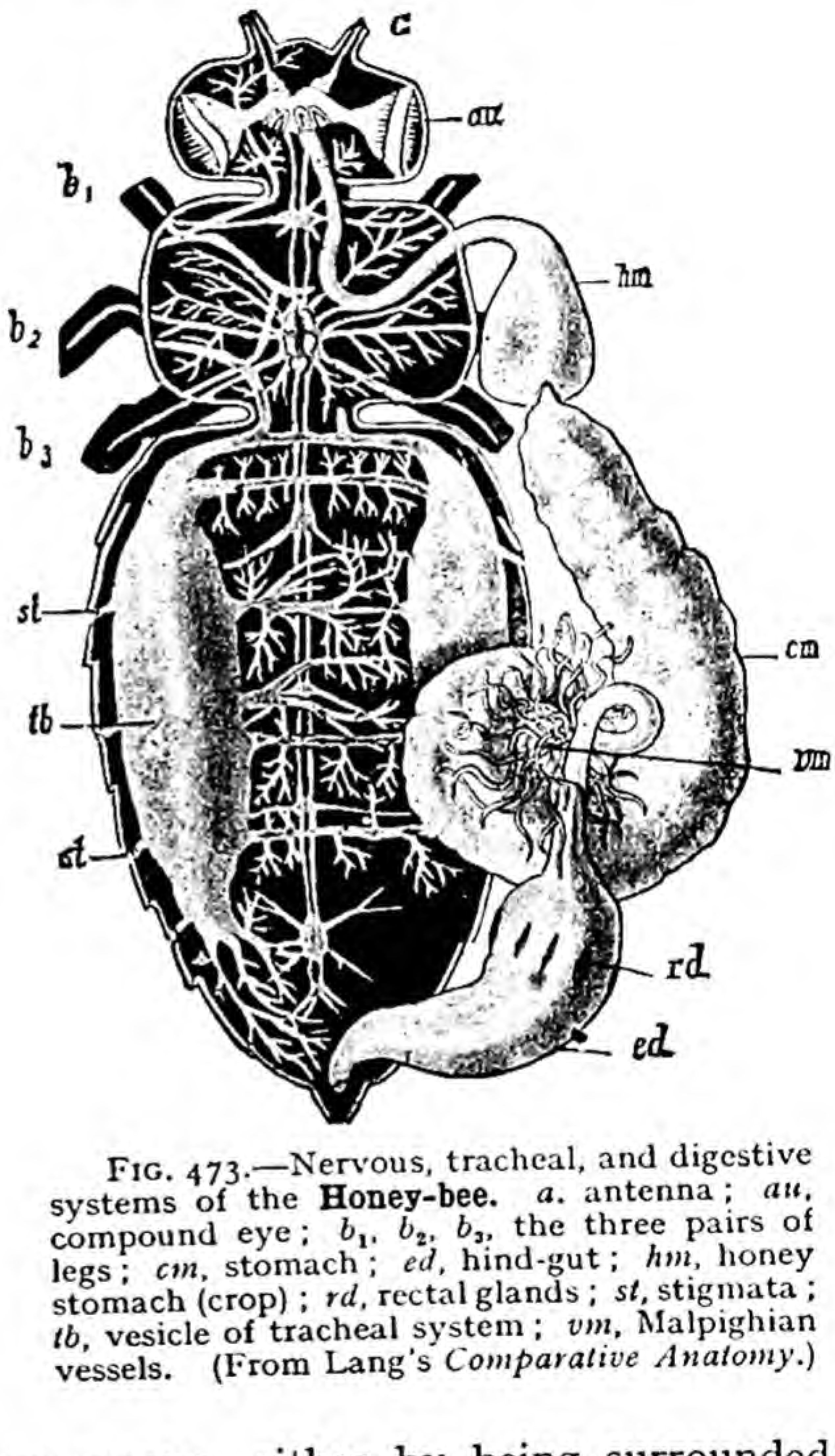


FIG. 473.—Nervous, tracheal, and digestive systems of the **Honey-bee.** *a*. antenna; *au*, compound eye; b_1, b_2, b_3, the three pairs of legs; *cm*, stomach; *ed*, hind-gut; *hm*, honey stomach (crop); *rd*, rectal glands; *st*, stigmata; *tb*, vesicle of tracheal system; *vm*, Malpighian vessels. (From Lang's *Comparative Anatomy*.)

entry of foreign particles by some means—either by being surrounded by special bundles of hairs, or by being provided with a special sieve-like membrane. In most cases they are capable of being closed by muscular action. In some Insects, mainly those adapted for active flight, such as the Hymenoptera, the tracheal system is dilated in certain parts of the body to form comparatively large *air-sacs* or *air-reservoirs* (*tb.*). In the aquatic larvæ of some Insects there is a series of soft external, simple or divided, processes—the *tracheal gills* (Fig. 474)—attached to the abdominal segments and richly supplied with tracheæ,

which have no communication with the exterior; in others *rectal gills* are developed—soft lamellæ on the inner surface of the rectum.

The **blood-vascular** system is, in comparison with the other systems of organs, not very highly developed, the need of an elaborate system of vessels being greatly diminished by the way in which all the tissues and organs are supplied with oxygen through the system of tracheæ. The blood is colourless

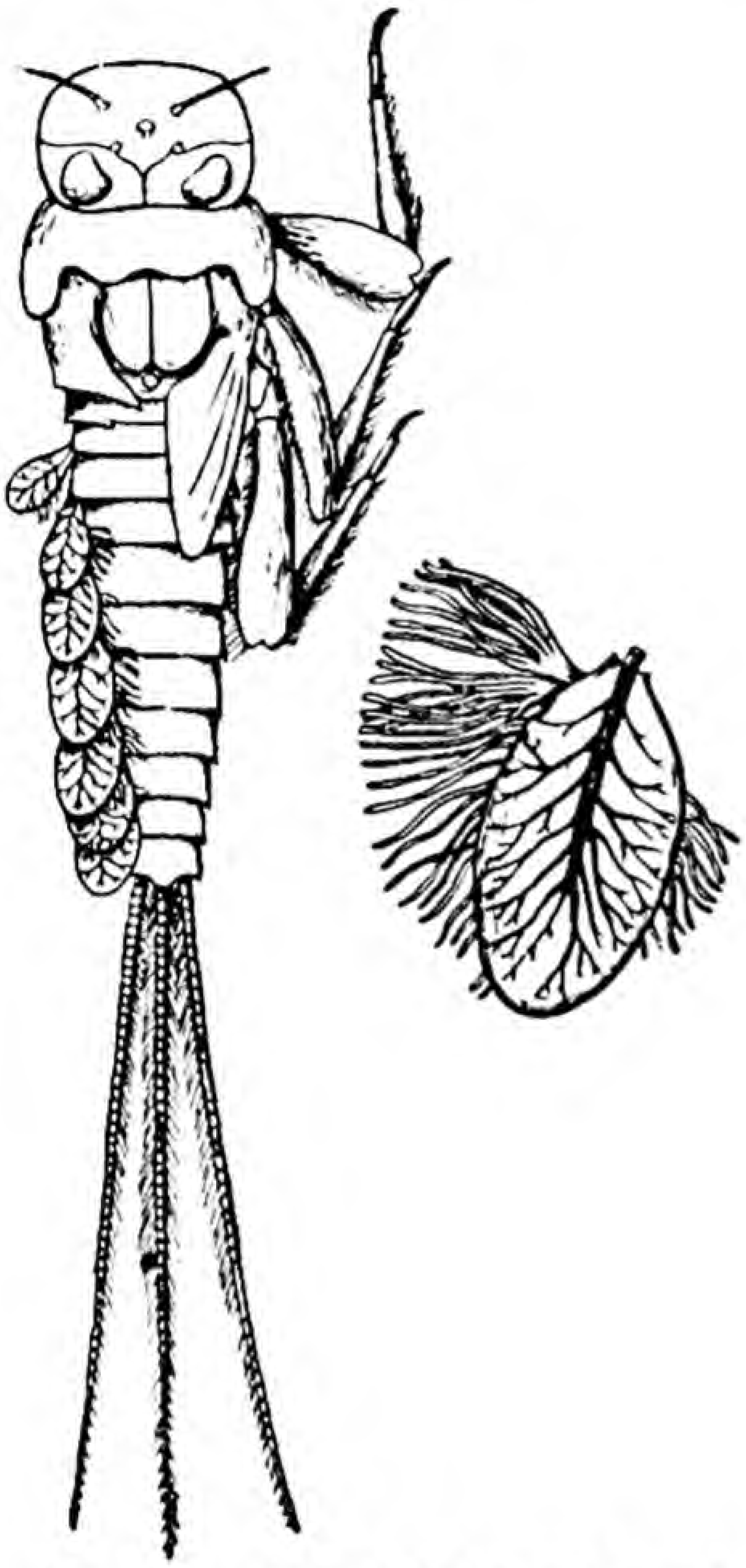


Fig. 474.—**Larval Ephemerid** with tracheal gills. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Vayssiere.)

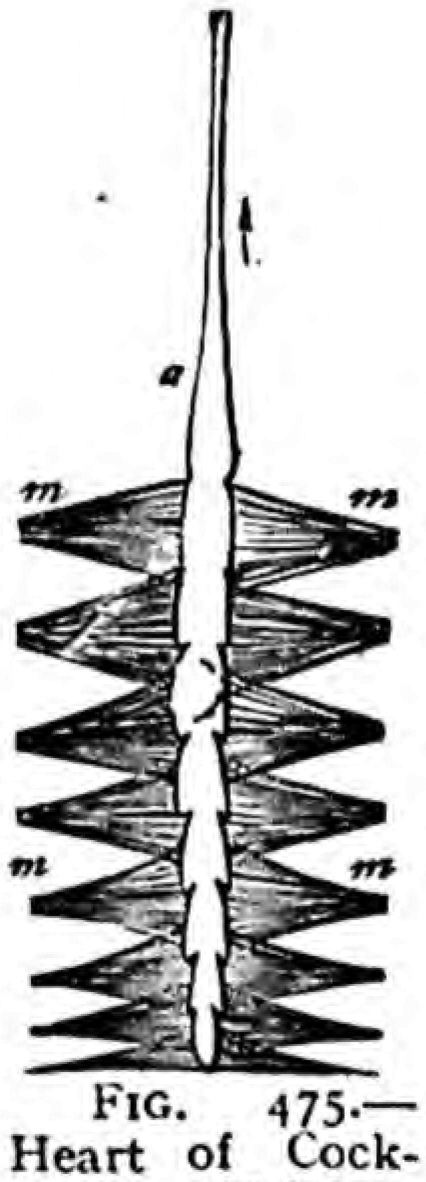


Fig. 475.—Heart of Cockchafer (**Melolontha**). *a*, aorta; *m*, *m*, alary muscles. (From Gegenbaur.)

or faintly yellowish or greenish, and contains colourless corpuscles. A contractile *dorsal vessel* or *heart* (Fig. 475) extends through the abdomen—and sometimes through the thorax—immediately below the terga. Its cavity is divided internally into a series of chambers by a system of valves. In its walls are a series of slits or *ostia*, by which a communication is effected between the internal cavity and a surrounding *pericardial sinus*. *Alary muscles*, fan-shaped bundles of fibres, arise from the terga and are in part inserted into the heart, causing or

assisting in causing its dilation and the opening of the *ostia*. In front the heart gives origin to a main vessel, or *aorta* (*a*).

The **nervous system** (Figs. 473 and 476) is on the same general plan as in the Crustacea. There is a double *supra-œsophageal ganglion* or *brain*, a *sub-œsophageal ganglion*, also double, and a series of *thoracic* and *abdominal pairs of ganglia*, which are closely united together in the middle line. The brain is relatively large in the higher Insects, and is divided into several lobes. It gives off nerves to the antennæ, the ocelli and the labrum, and on each side arises a large lobe—the *optic ganglion*—on which the compound eye rests. A pair of *œsophageal connectives* pass backwards on either side of the mouth from the

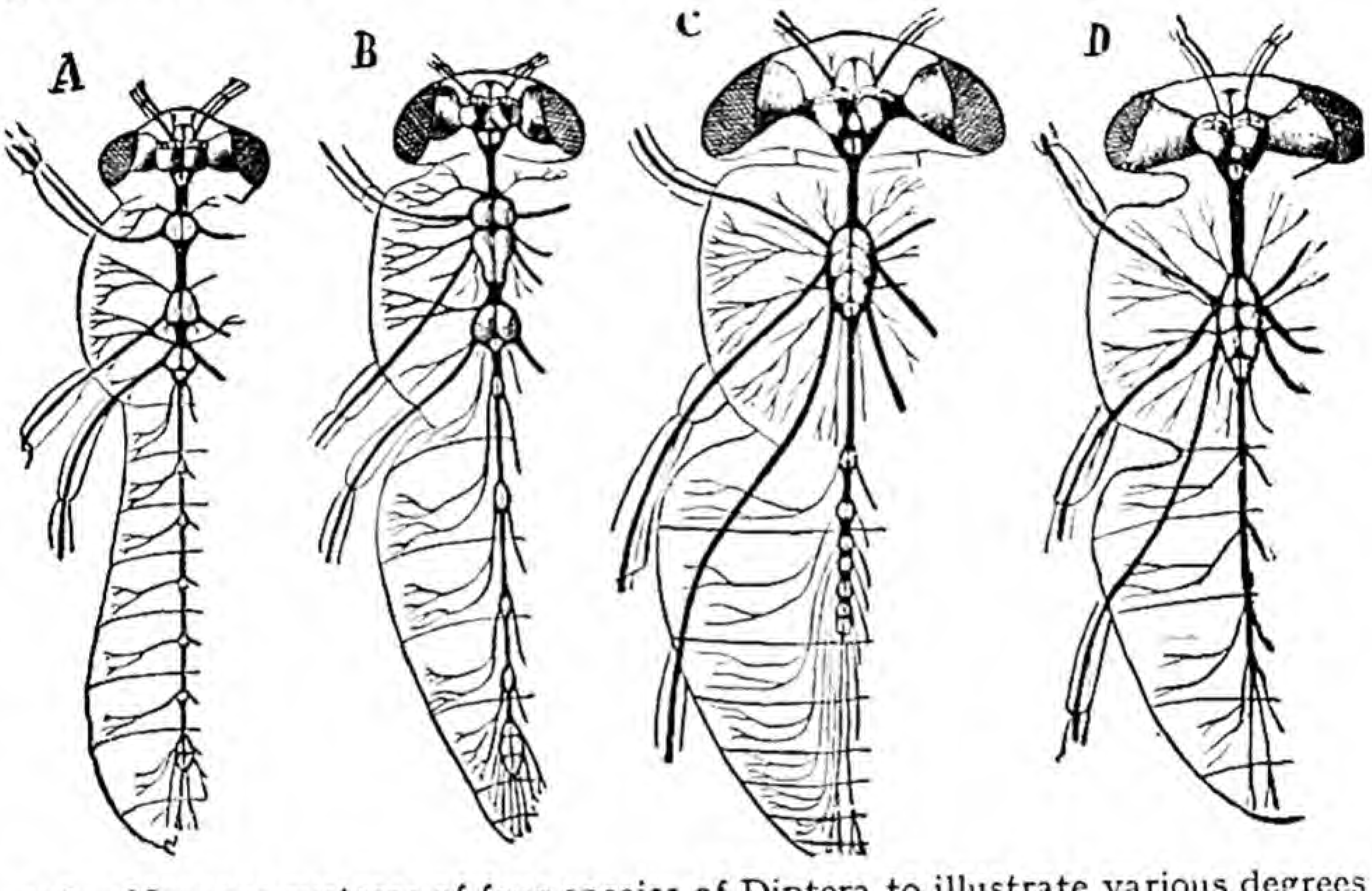


FIG. 476.—Nervous systems of four species of Diptera to illustrate various degrees of concentration. *A*, non-concentrated nervous systems of **Chironomus plumosus** with three thoracic and six abdominal ganglia; *B*, nervous system of **Empis stercorea** with two thoracic and five abdominal ganglia; *C*, nervous system of **Tabanus bovinus**, with one thoracic ganglion and with the abdominal ganglia closely approximated; *D*, nervous system of **Sarcophaga carnaria**, with all the ganglia of the ventral chain united together with the exception of the sub-œsophageal. (From Lang's *Comparative Anatomy*.)

brain to the sub-œsophageal ganglion. These connectives are usually very short, and, as a consequence, the brain and sub-œsophageal ganglia are closely approximated. From the latter there originate nerves to the appendages of the mouth—the mandibles and the two pairs of maxillæ. There are sometimes three pairs of thoracic and as many as eight of abdominal ganglia in the adult insect; but in many cases there is a greater or less degree of concentration of the ventral ganglionic chain (Fig. 476), and in some of the Diptera this reaches such an extreme that all the ventral ganglia, with the exception of the sub-œsophageal, are united into one elongated mass. The Insects, like the higher Crustacea, possesses a *visceral* or *sympathetic* nervous system, connected with the œsophageal connectives, and passing backwards on the œsophagus and crop.

The most highly developed sense-organs are the large compound *eyes.* The surface of the compound eye is marked out, as in the case of the Crayfish, into a great number of minute hexagonal facets, each of which indicates one of the elements (*ommatidia*) of the eye. Of these there may be as many as 28,000 (Dragon-fly). When the eye is examined in section, each *ommatidium* (Fig. 477) is found to consist of a *cornea-lens* (*l.*)—the outer surface of which forms the facet—a *crystalline cone* (*cc*), and a *rhabdome* (*rh*). The crystalline cone is not always developed, its place being taken in the eyes of some Insects by four *crystal cells.* The rhabdome is a compound rod formed by the union of sensory processes radiating from usually seven *retinula-cells* (*r.*) towards the centre of the ommatidium (*C*). Each retinula-cells is a *neurosensory cell* and as such is continuous with a nerve-fibre (*n.*). The sensory processes of the retinula-cells,

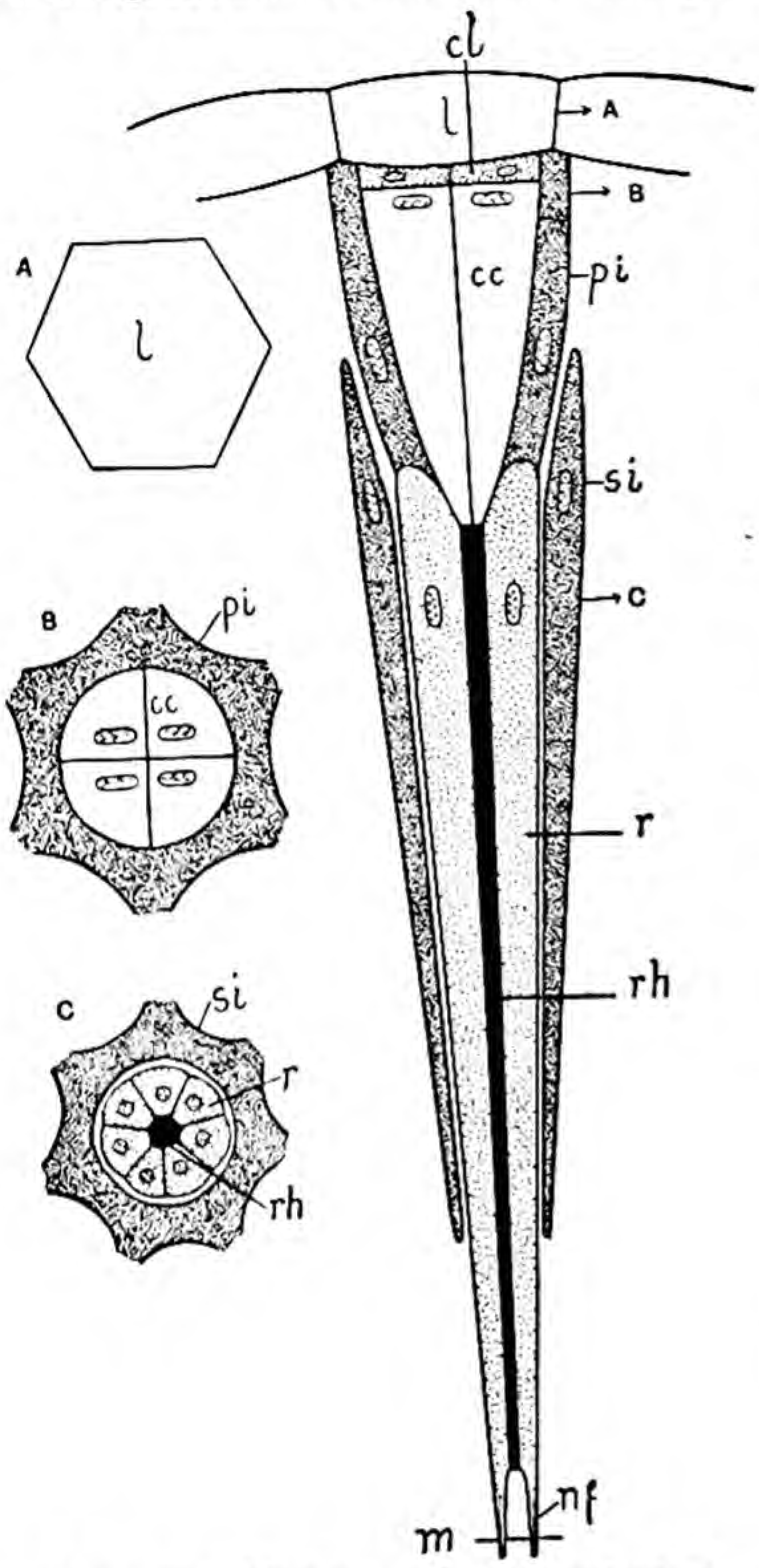


FIG. 477.—Diagram of a generalized **Ommatidium of an Insect-eye.** *cc.* crystalline cone; *cl.* corneagen layer; *l.* corneal lens; *m.* fenestral membrane; *nf.* nerve fibre; *pi.* primary iris cells; *r.* retinula; *rh.* rhabdom; *si.* secondary iris cells; *A*, *B*, and *C*, transverse sections of regions bearing corresponding lettering. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

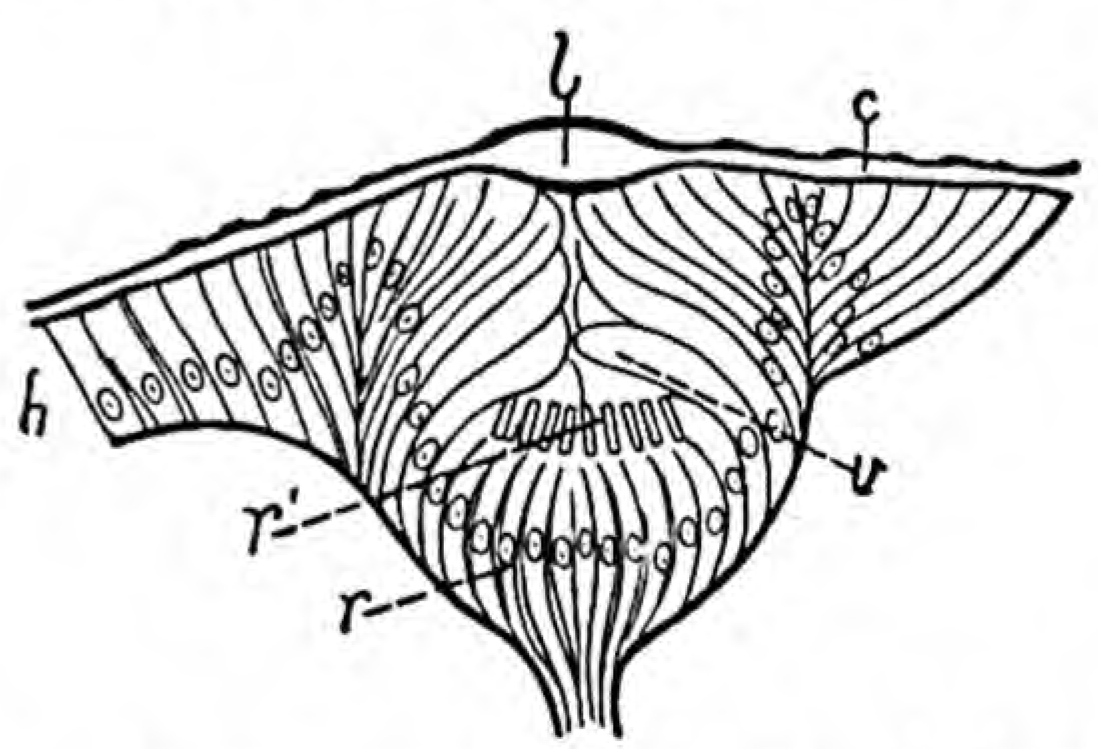


FIG. 478.—Section through the **Ocellus of a young Dyticus larva.** *c.* cuticle; *l.* lens; *h.* hypodermis; *r.* retinal cells with their rhabdoms, *r'.*; *v.* vitreous layer (modified hypodermal cells). (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Grenacher.)

which contribute to the formation of the rhabdome are called *rhabdomeres.* Beneath the rhabdomes is a *fenestrated membrane*, beneath which, again, is a dense plexus of the visual nerve-fibres. Pigment-cells (*pi.*, *si.*) surround the crystalline cones and retinulæ.

The *ocelli*, or simple eyes (Fig. 478), consist of a biconvex transparent thickening of the cuticle—the *lens*—and beneath it of a group of specially modified epidermal cells. Some of these, situated beneath the lens, form a transparent mass, the *vitreous body*, another set of elongated cells being arranged to form the *retina*.

The antennæ and palpi are the *organs of touch*, and these appendages are also the seat of the *olfactory sense*. A number of minute processes sometimes sunk in pits, and each having a special nerve-plate connected with it, are regarded as being specially concerned with this sense; and similar processes on the maxillæ and the epipharynx are perhaps connected with the *sense of taste*.

Peculiar sense-organs distinguished as *chordotonal* (Fig. 479) and *tympanal* organs (Figs. 480–482) occur in various parts of the body. The sensory elements in the chordotonal organs are spindle-shaped bundles of sensory cells (Fig. 479, *sc.*) with complicated auxiliary structures called *scolopales* (*s.*). They are part of a tense, chord-like structure attached at both ends to the hypodermis and extending across a certain region of the body cavity (*A*). Sometimes the basal end only is attached to the hypodermis, the apex ending free in the body cavity (*B*). The chordotonal organs are found in the legs and in the abdomen of both adult insects and larvæ. In their function they may be assumed to range from *proprioceptive* organs (*i.e.*, organs controlling limb posture and movement) to receptors for *mechanical* and *sound vibrations*. The tympanal organs (Figs. 480–482) are highly specialized auditory organs in which a group of similar sensillæ is in connection with a tense membrane or tympanum. Generally the tympanum (Fig. 482, *at.*, *pt.*) is in contact with a system of tracheal air-sacs (*ats.*, *pts.*) which function as auxiliary structures for the conduction of sound waves.

The name of *Johnston's organ* is given to organs of the chordotonal type which occur in the second segment of the antennæ in the majority of Insects.

In certain Insects—the Fireflies and Glow-worms, mostly belonging to the order Coleoptera—occur **luminous organs** for the production of light.

Sounds are emitted by many Insects, and are produced by a variety of different means. Often the sound is the result of the rubbing together of opposed rough surfaces of the integument. The chirp of the Grasshopper, for example, is produced by the rubbing of the femur of the last pair of legs over a series of ridges on the anterior wing, and that of the Locust by the rubbing against one another of the roughened basal parts of the first pair of wings. In other cases the sound results from the rapid vibratory movement of the wings; this is the case with the buzzing of many Diptera and Hymenoptera. Again, the humming sounds characteristic of many of the last-named order are produced partly by the vibrations of the wings in flight, partly by the vibration of leaf-like appendages in the tracheæ set in motion by strong expiratory

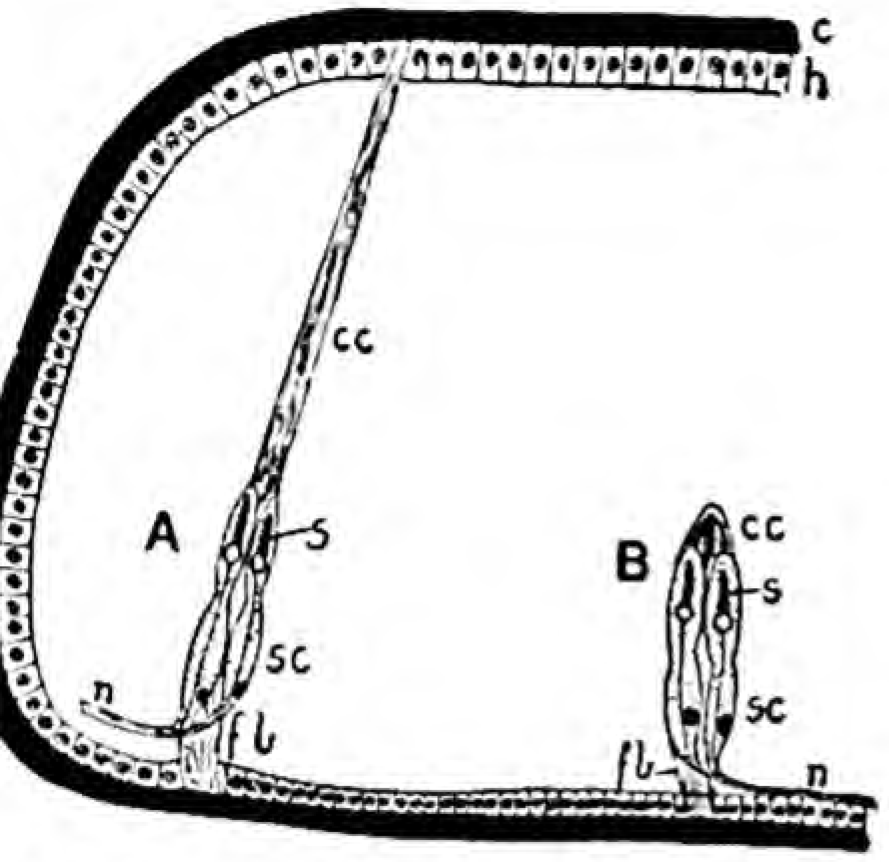


FIG. 479.—Diagram of two types of **Chordotonal Organs.** *A*, integumental, *B*, subintegumental. *c*. cuticle; *h*. hypodermis; *cc*. cap cell; *s*. scolopale; *sc*. sensory cell; *fb*. fibrillar binding tissue; *n*. nerve. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

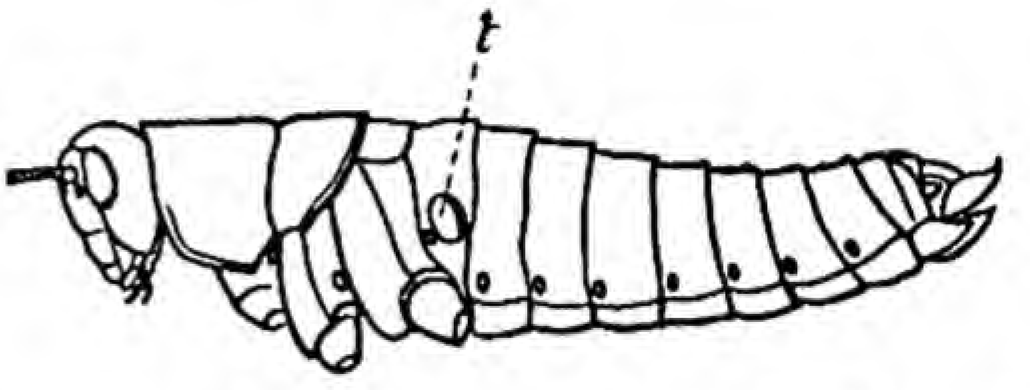


FIG. 480.—Lateral view of a **Locust** with wings and legs removed showing tympanum, *t*. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.), after Carpenter.)

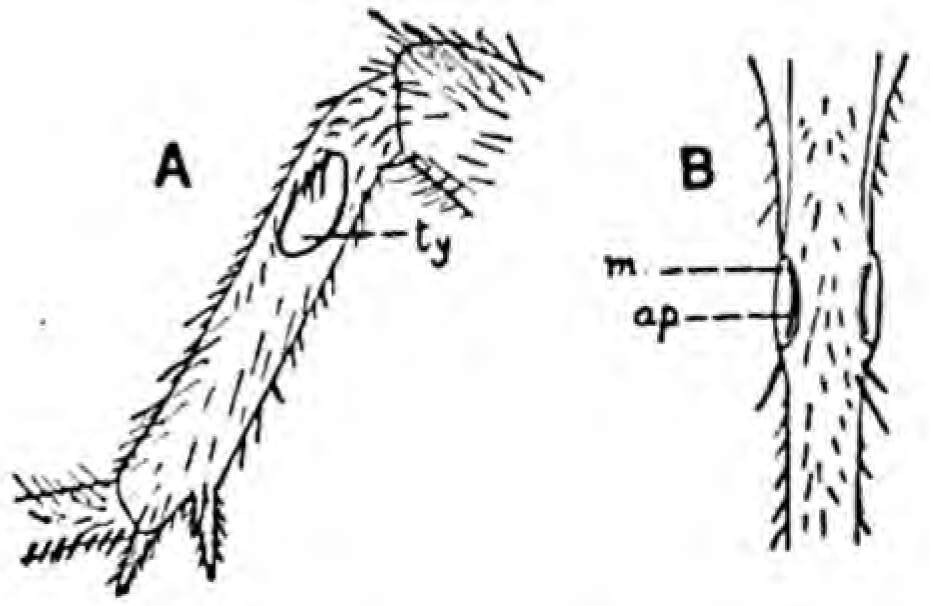


FIG. 481.—*A*, Left fore-tibia of **Gryllus domesticus** seen from the outside showing tympanum, *ty*. *B*, Portion of fore-tibia of **Locusta viridissima,** frontal view. *m*. membrane covering tympanum; *ap*. aperture into tympanal chamber. (From Imms's *A General Textbook of Entomology* (Methuen & Co., Ltd.).)

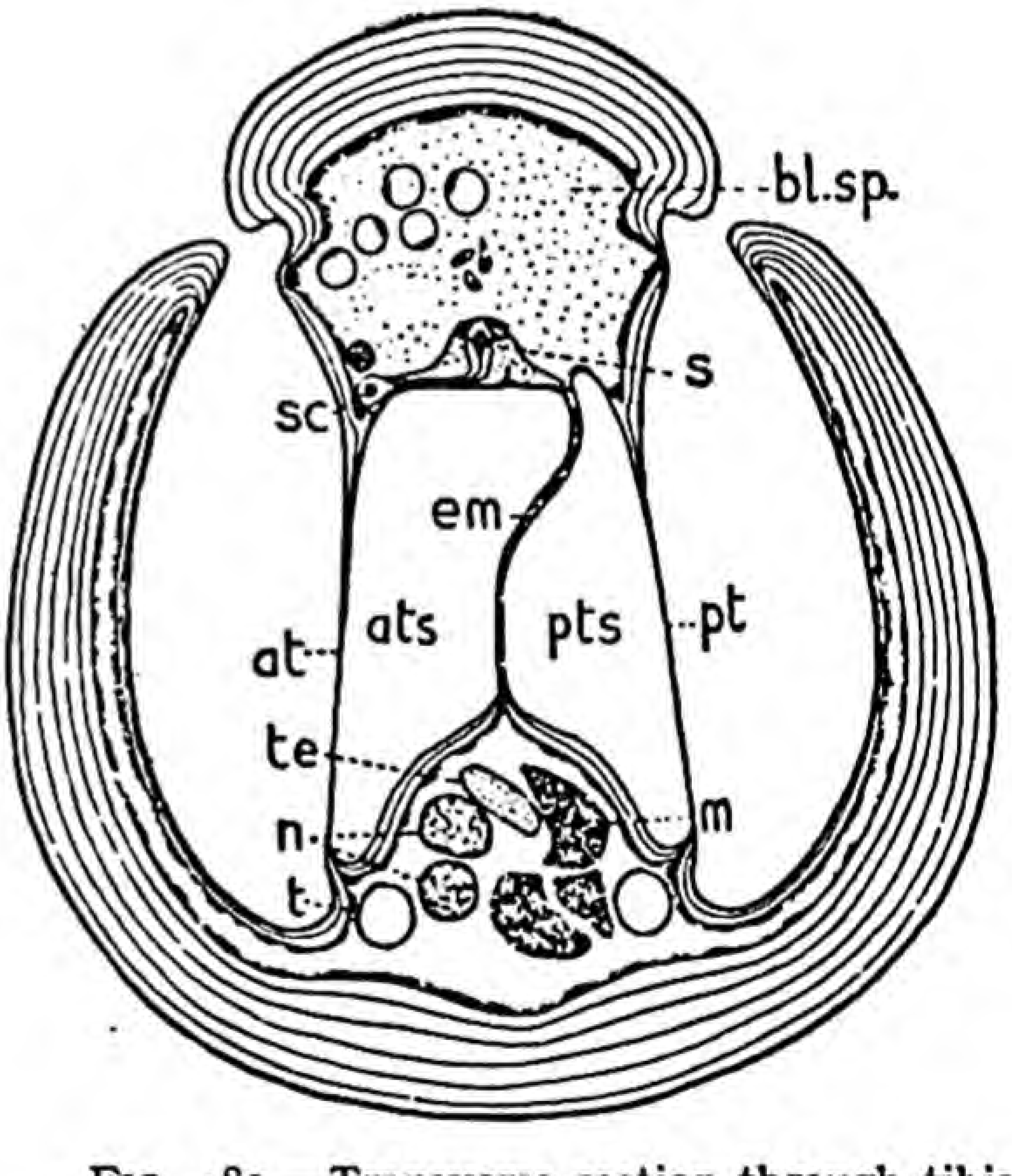


FIG. 482.—Transverse section through tibia of a **Locust,** containing tympanal organ. *at*. anterior tympanum; *ats*. anterior tracheal sac; *bl. sp*. blood space; *em*. elastic membrane; *m*. muscle; *n*. nerve; *pt*. posterior tympanum; *pts*. posterior tracheal sac; *s*. scolopale; *sc*. sensory cell; *t*. trachea; *te*. tendon. (From Weber's *Lehrbuch der Entomologie* (Gustav Fischer, Jena).)

currents of air. The loud shrill note of the Cicada is produced by the rapidly recurring contractions of the fibres of a muscle inserted into a stiff chitinous membrane, the result being a series of crackling sounds, which follow one another so rapidly as to give rise to a continuous note.

Reproductive organs.—The sexes are always separate in Insects, as in Arthropoda in general; and the males and females are very commonly distinguishable from one another by various modifications of form and of coloration. There are two *ovaries*, each of which consists of a greater or smaller number of narrow tubes or *ovarioles* (Fig. 483, *C*); in each of these the ova (*o.*)

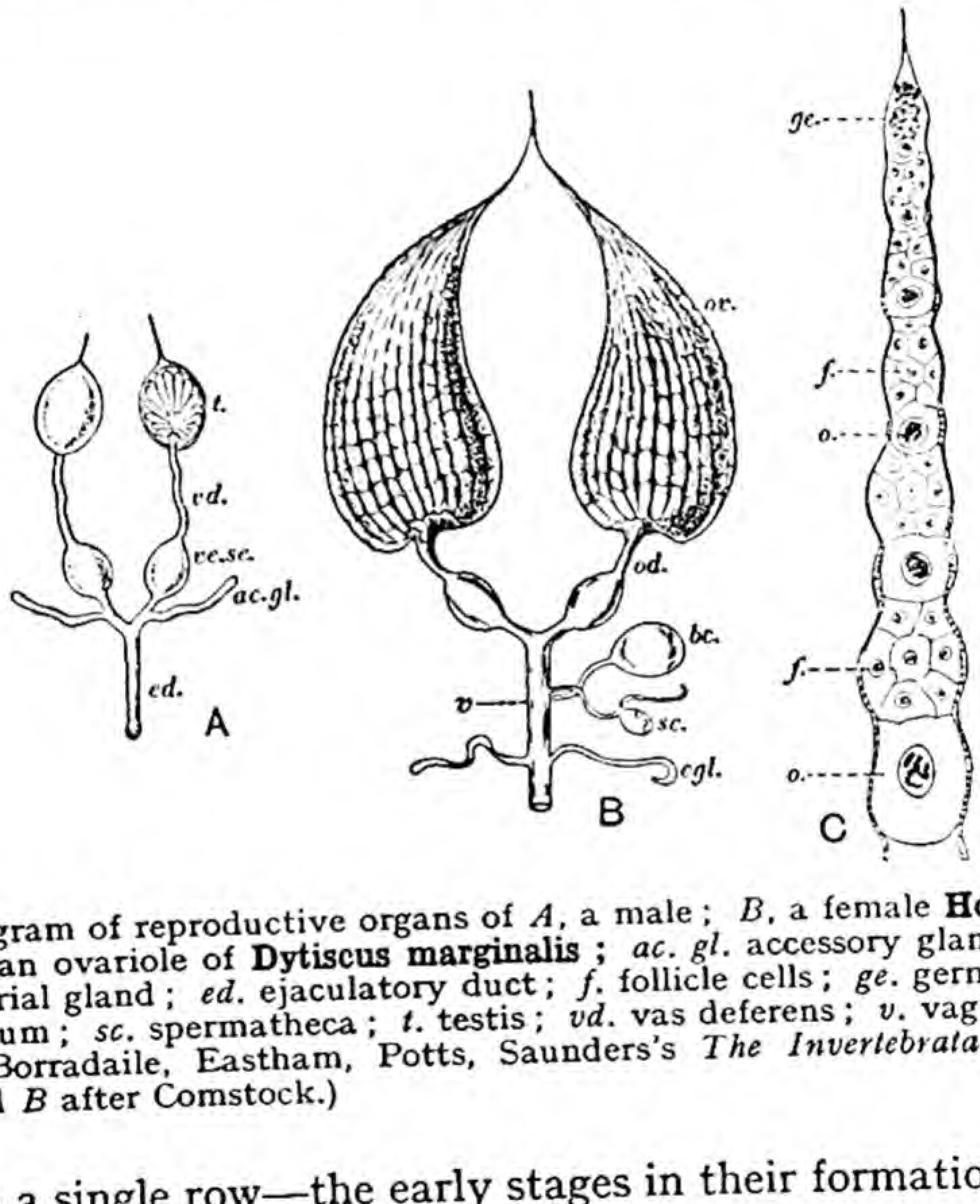


FIG. 483.—Diagram of reproductive organs of *A*, a male; *B*, a female **Honey-bee**; *C*, longitudinal section of an ovariole of **Dytiscus marginalis**; *ac. gl.* accessory gland; *bc.* bursa copulatrix; *cgl.* colleterial gland; *ed.* ejaculatory duct; *f.* follicle cells; *ge.* germarium; *ov.* ovary; *od.* oviduct; *o.* ovum; *sc.* spermatheca; *t.* testis; *vd.* vas deferens; *v.* vagina; *ve. se.* seminal vesicles. (From Borradaile, Eastham, Potts, Saunders's *The Invertebrata* (University Press, Cambridge), *A* and *B* after Comstock.)

are arranged in a single row—the early stages in their formation being situated in the germarium (*ge.*) at the anterior end, the more mature ova towards the posterior extremity. Follicle cells (*f.*) are also present, their arrangement within the ovariole varying in different groups. Each group of ovarian tubes opens into a lateral oviduct, and the two lateral oviducts, right and left (Fig. 483, *B*, *od.*), in most cases unite behind to form a median oviduct or vagina (*v.*), which opens towards the posterior end of the abdomen. Connected with this median oviduct, or opening close to it, are *receptacula seminis* (*sc.*) and *colleterial* or *cement-glands* (*cgl.*). Sometimes there is a copulatory sac, or *bursa copulatrix* (*bc.*). In the male the paired *testes* (*A*, *t.*) vary greatly in form: sometimes each is a long, narrow tube; sometimes several such tubes combine to form the

testis; or it may be of a more compact rounded form and entire or lobed. Each testis has a slender duct or *vas deferens* (*A*, *vd.*), the two vasa deferentia uniting to form a median *ejaculatory duct* (*ed.*). A *vesicula seminalis* (*ve. se.*) is appended to each vas deferens or to the ejaculatory duct. Accessory glands (*ac. gl.*), opening into the vas deferens or the ejaculatory duct, secrete cementing material for uniting the sperms into masses, the *spermatophores*. In most instances the eggs are laid shortly after their fertilization, only a comparatively few forms, such as the *Aphides* or Plant-lice, many Diptera, some Coleoptera and others, being *viviparous*. Some Insects, such as the Aphides, the social Hymenoptera, some Lepidoptera and others, present us with the phenomenon of *parthenogenesis*; *i.e.*, ova are formed, as in ordinary female insects, in organs corresponding to the ovaries of the latter, and are developed without fertilization.

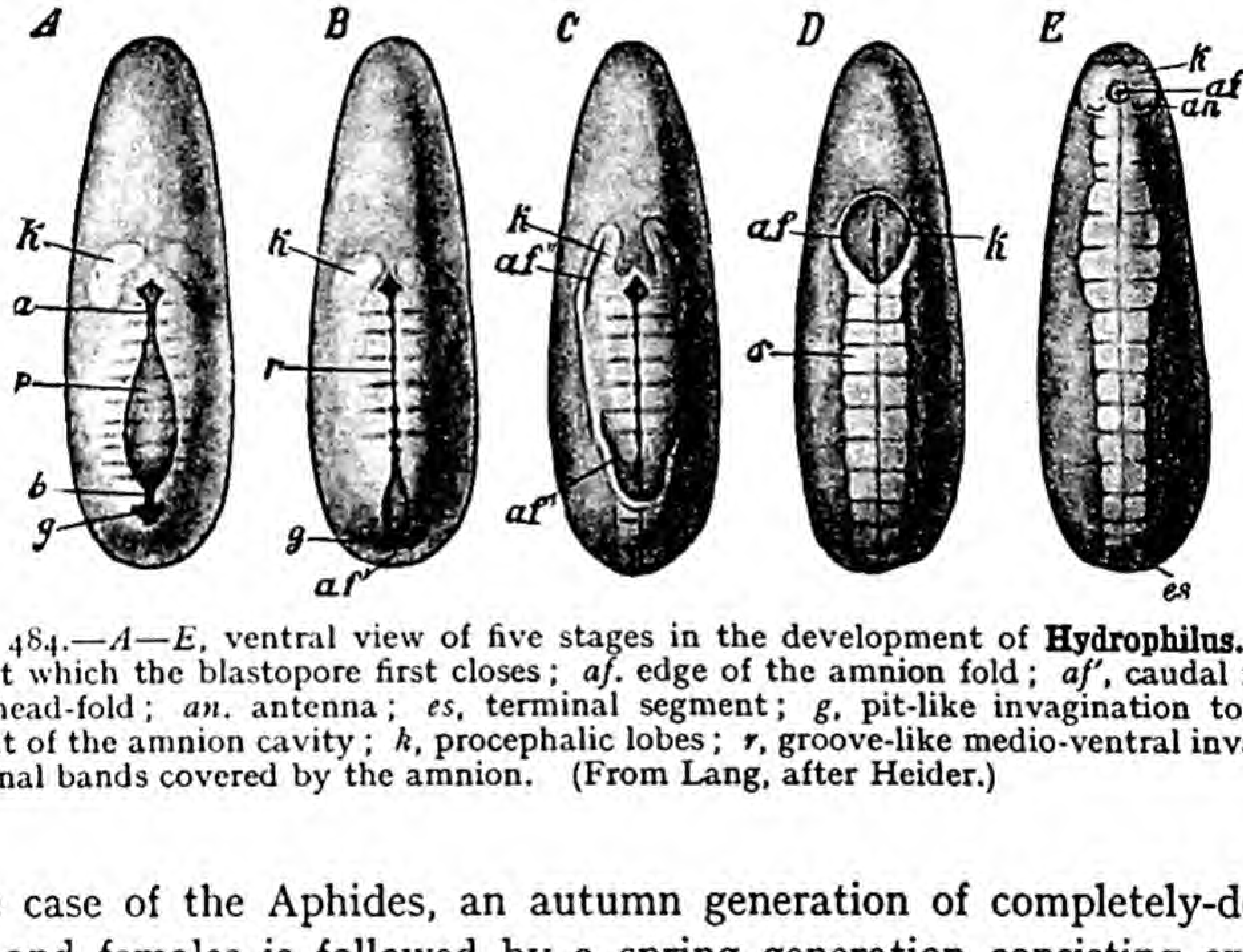


FIG. 484.—*A*—*E*, ventral view of five stages in the development of **Hydrophilus.** *a* and *b* points at which the blastopore first closes; *af*. edge of the amnion fold; *af'*, caudal fold; *af''*, paired head-fold; *an*. antenna; *es*, terminal segment; *g*, pit-like invagination to form the rudiment of the amnion cavity; *k*, procephalic lobes; *r*, groove-like medio-ventral invagination; *s*, germinal bands covered by the amnion. (From Lang, after Heider.)

In the case of the Aphides, an autumn generation of completely-developed males and females is followed by a spring generation consisting entirely of females; these are both parthenogenetic and viviparous. In the Honey-bee fertilized eggs develop into females, whereas unfertilized eggs develop parthenogenetically into males. *Pædogenesis* accompanies parthenogenesis in certain Diptera; *i.e.*, the *larvæ* or *pupæ* produce ova and embryos without fertilization.

The **eggs** when laid are protected from injury by a number of methods; they may be firmly fixed to the substratum, buried in the earth, or laid in the interior of certain plants or even of animals. The deposition of the eggs, by means of ovipositors, in the leaves or other parts of plants gives rise to swellings—the so-called *galls*, in the interior of which the young Insects live. In the case of many Insects the eggs are enclosed in a cocoon; in others they are surrounded by a gelatinous or waxy material. The eggs are, for the most part,

of relatively considerable size. In form they vary, but the long oval prevails in most instances. The ripe egg is enclosed in two egg-membranes—an inner, the *vitelline membrane*, produced by the egg itself, and an outer, the *chorion*, formed from the follicle-cells. The chorion, which usually exhibits a more or less elaborate pattern, has one or more apertures or micropyles for the entry of the sperm. The contents are distinguishable into two layers—a superficial, consisting of protoplasm, and a central, of nutrient yolk.

Development.—The early development has already been described in the case of the Cockroach (p. 473) and is similar in most members of the class. The same holds good of the formation of the amnion and the further development of the mesoderm and endoderm. In some cases there is developed between the serosa and the true amnion a space filled with yolk, and the ventral plate appears sunk within the yolk. The nervous system is developed from the ectoderm in the manner indicated in the account of the Cockroach (p. 476). The tracheal system is derived from a series of pairs of segmentally arranged ectodermal involutions (Fig. 485, *st*).

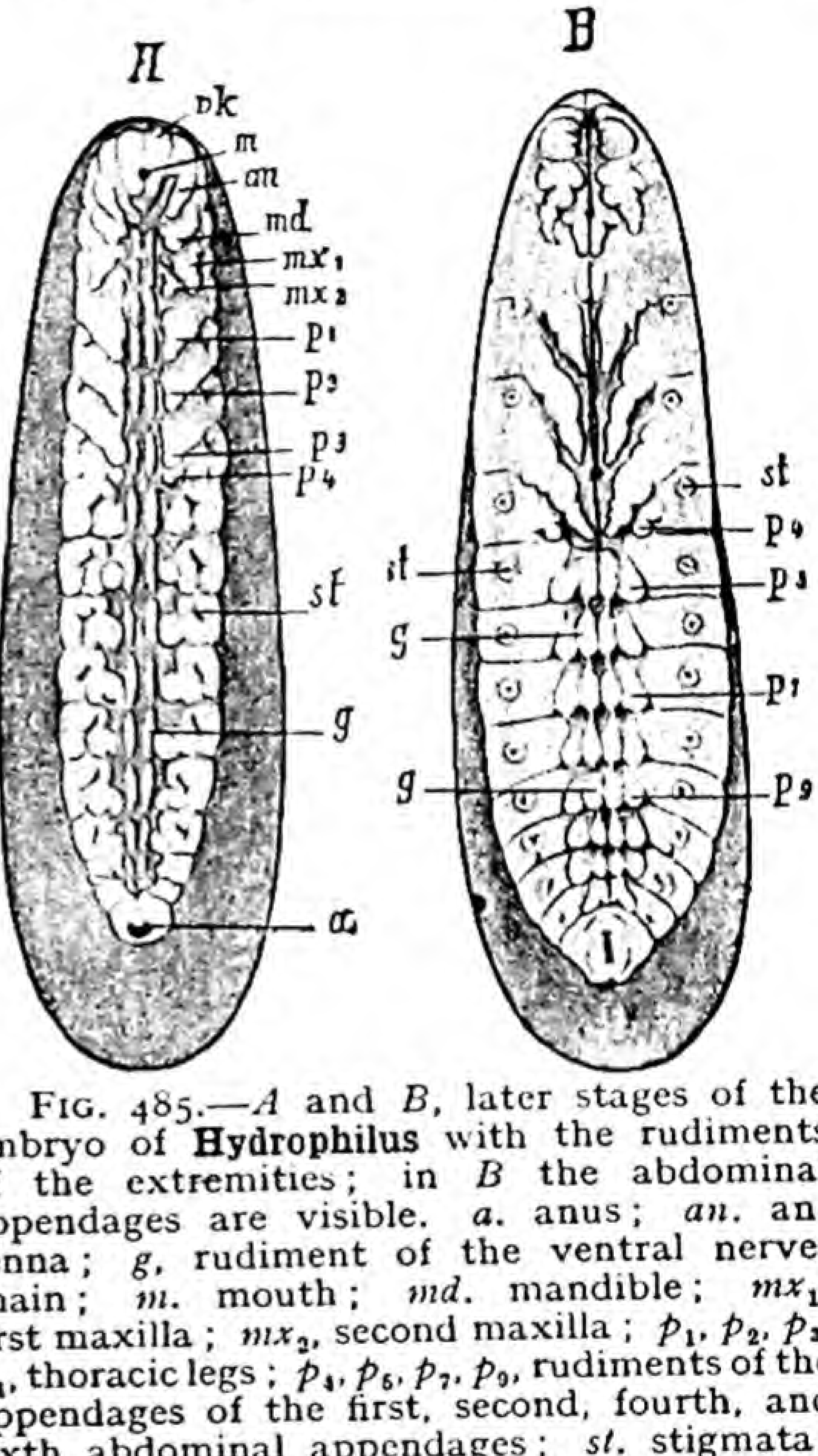


FIG. 485.—*A* and *B*, later stages of the embryo of **Hydrophilus** with the rudiments of the extremities; in *B* the abdominal appendages are visible. *a*. anus; *an*. antenna; *g*. rudiment of the ventral nerve-chain; *m*. mouth; *md*. mandible; mx_1, first maxilla; mx_2, second maxilla; p_1, p_2, p_3, p_4, thoracic legs; p_4, p_5, p_7, p_9, rudiments of the appendages of the first, second, fourth, and sixth abdominal appendages; *st*. stigmata; *vk*, prostomium. (From Lang, after Heider.)

Metamorphosis.—In some instances the young Insect, when it escapes from the egg-membranes, has exactly the form of the parent, except that, as a rule, the wings have not yet grown. But in most cases there is a metamorphosis. In some this is comparatively slight and gradual, the adult Insect differing from the larva only in comparatively unimportant points, and the segments and appendages of the latter becoming directly converted into those of the former. Such a metamorphosis, in which there is no quiescent stage, is said to be *incomplete*. The term *complete* is applied to the metamorphosis of the majority of Insects, in which the larva differs so completely from the *imago*, or perfect Insect, in external form, the nature of the appendages, and the internal organization, that there is need of a quiescent or *pupa* stage, during which the whole animal, or a considerable part of it, undergoes an entire transformation. The Insects with incomplete metamorphosis form the division *Exopterygota* or

Heterometabola, whereas the Insects with complete metamorphosis are included in the division *Endopterygota* or *Holometabola* of the sub-class *Pterygota*. In many Diptera the body of the larva or "maggot" is completely worm-like, without any appendages, and without any distinct head. In other cases (Lepidoptera, etc.) there is a distinct head; the three thoracic segments have three pairs of jointed legs, and the abdominal segments short unjointed *pro-legs* (Fig. 458). In most instances the larvæ differ widely from the adults in their food and mode of life; very generally the jaws are adapted for biting, even when the mouth of the adult is suctorial. After a longer or shorter period passed in this larval condition, in which it is usually active and very voracious, the young Insect passes into a quiescent or *pupa* stage, during which it remains passive, enclosed in a tough integument, while a more or less complete reconstruction of the organs goes on, resulting in the development of all the parts of the perfect Insect. The development of the new parts takes place from certain patches of cells, the *imaginal discs*, present in the larva.

In the Diptera the larva or maggot is sometimes completely devoid of jaws. In some Diptera, however, the jaws are well developed, and there is a distinct head. After frequent moultings the maggot passes either into a quiescent or pupa stage enclosed in a hard skin, or into the stage of an active *aquatic pupa*, which swims about actively in water and may possess tracheal gills.

Lepidopterous larvæ are often brilliantly coloured, are very active, and feed with voracity, chiefly on leaves and other succulent parts of plants. Eventually they spin a cocoon of a silky substance, enclosed within which, and covered with a tough skin, they pass through a quiescent or pupa condition—the condition—of the *chrysalis* (Fig. 458). From the interior of this the imago subsequently emerges with all the parts of the adult Insect fully formed.

In **mode of life** there is a very considerable difference between different orders and families of Insects. Some are parasites in the strict sense throughout life. This is the case, for instance, in the Strepsiptera (Bee-parasites), the females of which live permanently lodged between the joints of the abdomen of their hosts. The Lice and Bird-lice are external parasites throughout life; Bugs and Fleas, though not adhering to their hosts, are parasites as regards their diet. Many Insects are parasites in the larval condition, though free in the adult state. This holds good, for example, of the larvæ of the Ichneumons, which develop in the interior of the bodies of other insect-larvæ; also of the larvæ of the Bot-flies (Fig. 464), which inhabit the alimentary canal of mammalian hosts (Horses, Oxen, Sheep, Rhinoceroses, Tapirs). The blood-sucking Insects act in certain cases as the carriers or intermediate hosts of the protozoan or bacterial parasites that are the causes of various diseases in man. Thus, as was stated in the account of the malaria-parasite (Section II, p. 85), mosquitoes are the means of conveying that disease from one person to another.

In accordance with the high grade of the structure of their various systems

of organs, Insects exhibit a correspondingly high degree of functional activity. The quantity of food consumed and assimilated is great in comparison with the bulk of the body, and the energy expended in muscular contractions is of very considerable amount. It is estimated that while the muscular force exerted by a Horse bears a ratio of about 0·7 to its own weight (reckoned as 1) the muscular force of an Insect bears a ratio to its weight of from about 14 to about 25. Insects are also distinguished among the Invertebrata by the keenness of their senses. The sense of sight is, as we should expect from the elaborate

FIG. 486.—**Apis mellifica.** *a*, queen; *b*, worker; *c*, drone.
(From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer).)

character of the optic organs, most highly developed, many Insects having been shown by experiment to have a keen sense of colour; but a sense of smell, the seat of which is in the antennæ and palpi, can be shown to exist in a high degree, and the parts about the mouth bear nerve-endings concerned in a well-developed sense of taste, similar sense-organs being found on the tarsi of some Diptera and Lepidoptera. A sense of hearing does not appear to be universally present, but is well marked in such forms as produce sounds. At the same time Insects are remarkable for the instincts, often leading to results of an elaborate character, which guide them in the pursuit of food and the protection

FIG. 487.—Red Ant (**Formica rufa**); male, worker, and female. (After Brehm.)

and rearing of their young. Among the insects which are the most highly endowed in this respect are some—the Termites, Bees, Wasps, and Ants—which live together in organized associations or communities, the various individuals composing which are distinguishable into *sexual individuals*, *neuter workers*, and *soldiers* (Figs. 438, 486 and 487), each specially organized for the part which it has to play in the economy of the community.

Distribution in time.—The earliest known fossil remains of Insects have been found in rocks of Ordovician age. A good many fossil Insects have been found in the Devonian; but they only become abundant in the Carboniferous.

All the Palæozoic Insects have been regarded by some as belonging to a single, distinct order, which has been named the *Palæodictyoptera*. The members of this group are characterized rather by the absence of the special characteristics of any of the existing orders than by any positive features of their own; but different families of the order approximate to a certain extent towards the groups of living Insects. Amongst them, for example, are forms representing the Cockroaches and the Phasmidæ among the Orthoptera; others representing the modern May-flies; others the Coleoptera. This view, however, is not held by all Palæontologists.

Of the existing orders, the Neuroptera, Orthoptera, Hemiptera, and Coleoptera are first found in the Triassic or in the Permian; the Diptera, Hymenoptera and Lepidoptera in the Jurassic.

CLASS IV.—ARACHNIDA.

The class *Arachnida*, comprising the Scorpions and Spiders, the Mites and Ticks, the King-crabs, and a number of other families, is a much less homogeneous group than the Insecta, approaching the Crustacea in the variety which it presents in the arrangement of the segments and their appendages. In most members of the class, however, there is an anterior region of the body—the *cephalothorax* (*prosoma*)—representing both head and thorax, and a posterior part, or *abdomen* (*opisthosoma*), which is typically composed of a number of distinct segments; in some cases cephalothorax and abdomen are amalgamated.

There are no antennæ. The first pair of appendages of the cephalothorax are the *chelicerœ*; the second are the *pedipalpi*. Behind these are four pairs of legs. The organs of respiration are sometimes tracheæ, similar to those of the Insects, sometimes book-lungs—sacs containing numerous book-leaf-like plates: sometimes leaf-like external appendages or gills.

1. Example of the Class.—The Scorpion (*Euscorpio* or *Buthus*).

Scorpions are inhabitants of warm countries—the largest kinds being found in tropical Africa and America. They are nocturnal animals, remaining in holes and crevices during the day, and issuing forth at night to hunt for their prey, which consists of Spiders and Insects. These they seize with their pincer-claws and sting to death with their caudal spine, afterwards sucking their juices.

There are a number of different species of Scorpions, divided into several genera, which differ from one another in comparatively unimportant points, so that the following general description will apply almost equally well to any of them.

External features.—A Scorpion (Fig. 488) has a long narrow body, in superficial appearance not unlike that of a Crayfish. There is a small cephalothoracic

shield or *carapace*, covering over dorsally a short anterior region—*cephalothorax* or *prosoma*. This is followed by a long posterior region or *abdomen* (*opisthosoma*), the terminal part of which in the living animal is habitually carried over the back (Fig. 500), constituting the "tail," at the end of which the sting is placed.

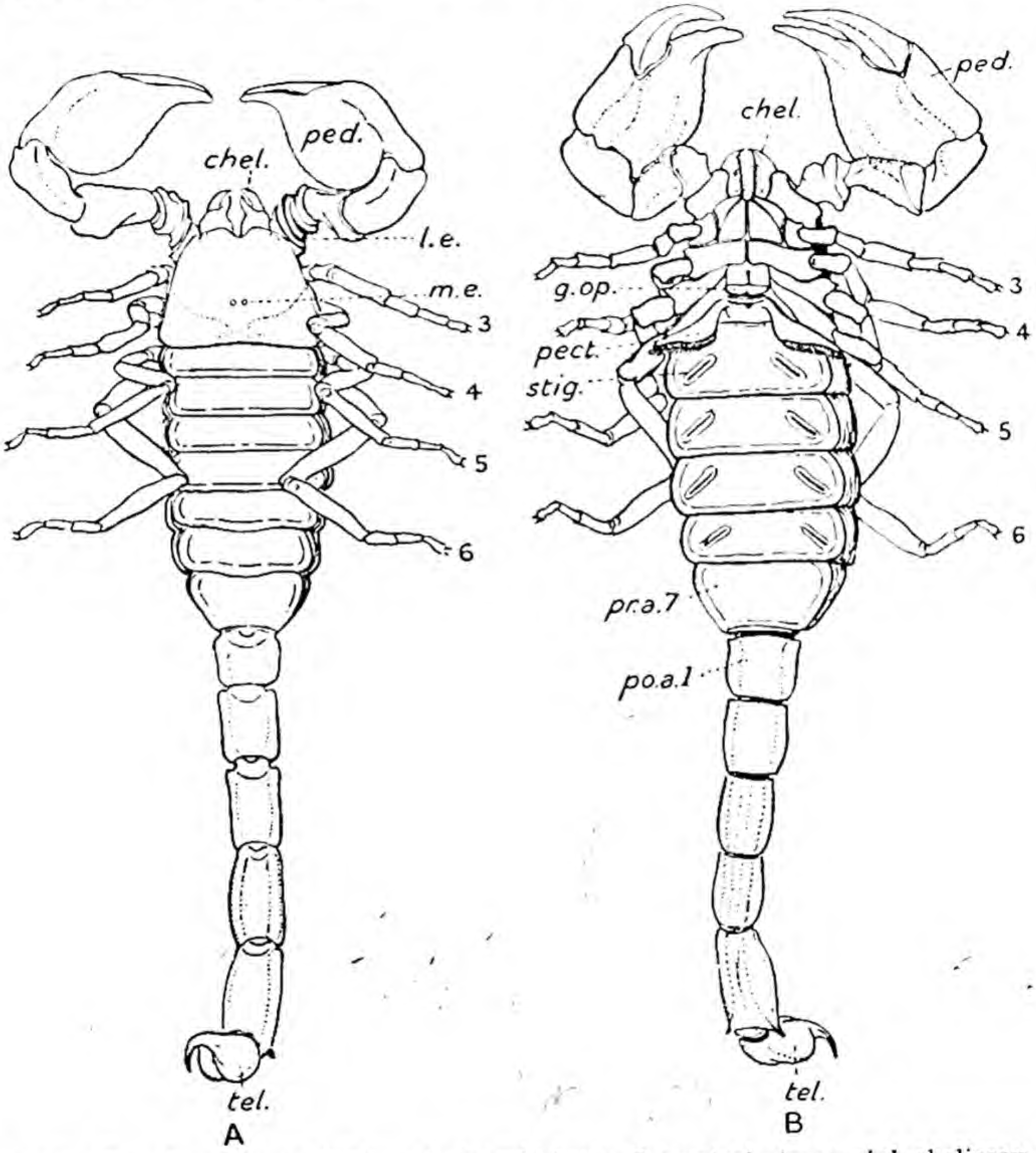


FIG. 488.—**Scorpio swammerdami.** *A*, dorsal view; *B*, ventral view; *chel.* cheliceræ; *g. op.* genital operculum; *l. e.* lateral eyes; *m. e.* median eyes; *pect.* pectines; *ped.* pedipalpi; *pr. a. 7* last segment of pre-abdomen (first segment of metasoma); *po. a. 1* first segment of post-abdomen (second segment of metasoma); *stig.* stigma; *tel.* telson; *3, 4, 5* and *6*, walking legs. (From Shipley and MacBride's *Zoology* (University Press, Cambridge).)

The carapace bears a pair of large eyes about its middle, and several pairs of smaller eyes on the antero-lateral margin. The aperture of the *mouth*, which is very small, is at the anterior end of the cephalothorax on its ventral aspect; a lobe which overhangs it in front is the *labrum*. On each side of the mouth is a three-jointed appendage—the *chelicera* (Fig. 488, *chel.*)—which is terminated by

a chela. Behind these are the very large *pincer-claws* or *pedipalpi* (*ped.*), each composed of six podomeres and terminating in a powerful chela. The basal joint of each pedipalp has a process which bites against the corresponding process of the other pedipalp, these processes thus performing the function of jaws. Following upon the pedipalpi are four pairs of walking legs, each composed of seven podomeres, the last of which is provided with curved and pointed horny claws. The basal segments of the first two pairs of walking legs are modified so as to perform to some extent the function of jaws.

The six pairs of appendages hitherto described—the cheliceræ, the pedipalpi, and the four pairs of walking legs—belong to the cephalothorax or prosoma. The cephalothorax is formed by the fusion of the anterior *pre-segmental region* with originally seven segments, of which the first—the so-called *precheliceral segment*—exists only for a short period in early embryonic life.

The anterior broader part of the abdomen which is termed *pre-abdomen* consists, in the adult animal, of seven segments, each of which is enclosed in firm chitinous dorsal and ventral plates, or *terga* and *sterna*. The tergum and sternum of each segment are separated from one another laterally by intervals of soft skin. Originally there are eight segments, but the original first—the *pre-genital* segment—loses its distinctness during embryonic life. The posterior narrower part of the abdomen, which is termed *post-abdomen*, consists of five segments, each enclosed in a complete investing ring of hard chitinous matter. Articulating with the last segment of the post-abdomen is a *telson*, called *caudal spine* or *sting*, swollen at the base and acutely pointed at the apex, where open the ducts of two poison glands. The anal opening is situated on the ventral surface of the last segment of the post-abdomen, immediately in front of the sting.

The abdomen has also been described as subdivided into an anterior *mesosoma* and a posterior *metasoma*, and for morphological reasons each of these two regions should be described as consisting of six segments. In this case the tapering seventh segment of the pre-abdomen (Fig. 488 B, *pr. a. 7*) which differs from the preceding segments in the absence of stigmata and pulmonary sacs (*vide infra*) should be called the first segment of the metasoma. In view of the fact, however, that the segment does not take part in the upward curvature of the post-abdomen and that it differs from the following segments in having a distinct tergum and sternum, this mode of description is often not adopted, and the two terms mesosoma and metasoma are used as homologous with pre-abdomen and post-abdomen. There is thus no complete agreement as to the correct morphological significance of the seventh abdominal segment which might be described as transitional between the anterior and posterior regions of the abdomen.

The first segment of the pre-abdomen has a narrow sternum, on which there is a soft rounded median lobe divided by a cleft; this is termed the *genital*

operculum (*g. op.*); at its base is the opening of the genital duct. To the sternum of the second segment of the pre-abdomen are attached a pair of remarkable appendages of a comb-like shape—the *pectines* (*pect.*)—each consisting of a stem, along the posterior margin of which is a row of narrow processes, somewhat like the teeth of a comb. These appendages are derived from embryonic limb-rudiments and are tactile sense-organs. The remainder of the segments of the pre-abdomen, and all those of the post-abdomen, are devoid of appendages. The sterna of the third, fourth, fifth, and sixth segments of the pre-abdomen, which are very broad, bear each a pair of oblique slits—the *stigmata* (*stig.*)—leading into the pulmonary sacs.

FIG. 489.—Endosternite of **Scorpion.** (After Lankester.)

In the interior of the cephalothorax, over the nervous system is a cartilaginous plate—the *endosternite* (Fig. 489)—which serves to give attachment to muscles, and is comparable to the cephalic apodeme of Apus (p. 391).

The appendages of the cephalothorax of the Scorpion differ greatly from the corresponding appendages in the other Arthropods. The most anterior appendages—the *cheliceræ*—are pre-oral in position, the second pair—the *pedipalpi*—are post-oral.

Digestive system.—The narrow mouth leads into a large chamber with elastic walls, the *pharynx*; this is capable of being greatly dilated by the action of a number of radiating bundles of muscular fibres which run outwards from it to the walls of the cephalothorax, the result of this being to cause suction through the mouth, by which means the juices of the Scorpion's prey are drawn in. A second dilatation, to which a narrow œsophagus leads, receives the ducts of a pair of *salivary glands* (Fig. 491, *sal. gld.*). Upon this follows the *mesenteron* (*mesent.*), which is an elongated, wide, straight tube, with glandular walls, corresponding to the stomach of the Insect. Opening into the mesenteron are five pairs of narrow tubes (Figs. 490 and 491, *hep. du.*) leading into the substance of a large glandular body, usually termed the *liver* (Fig. 491, *hep.*), though its hepatic functions are doubtful. Into the long narrow intestine, in the last segment of the pre-abdomen, open one or two pairs of delicate tubes—the *Malpighian tubes* (*mal.*)—which act as the organs of renal excretion.

Circulatory organs.—An elongated tubular *heart* (Fig. 490, *hrt.*) lies in the pre-abdomen enclosed in a pericardial sinus; it is divided internally by folds into a series of eight chambers; into each of these chambers the blood passes by a pair of valvular apertures or *ostia*. The heart ends both in front and behind in main arteries, the *anterior* and *posterior aortæ* (*ant. art.*, *post. art.*); and a series of pairs of lateral arteries are given off from the various chambers. The anterior aorta soon bifurcates to form a pair of vessels which embrace between them the œsophagus, and meet below in a median ventral trunk which

runs backwards above the nerve-cord. The blood carried to the various parts of the body by the arteries is gathered up into a large ventral sinus from which it passes to the book-lungs. From these it is carried by a series of veins to the pericardial sinus to enter the heart through the ostia.

The **organs of respiration** in the Scorpions are in the form of *pulmonary sacs* or *book-lungs* (*pul.*), the stigmata or external openings of which have already been referred to. Each pulmonary sac is a compressed chamber lined with a thin cuticle. The lining membrane is raised up into numerous delicate laminæ lying parallel with one another like the leaves of a book. Into the

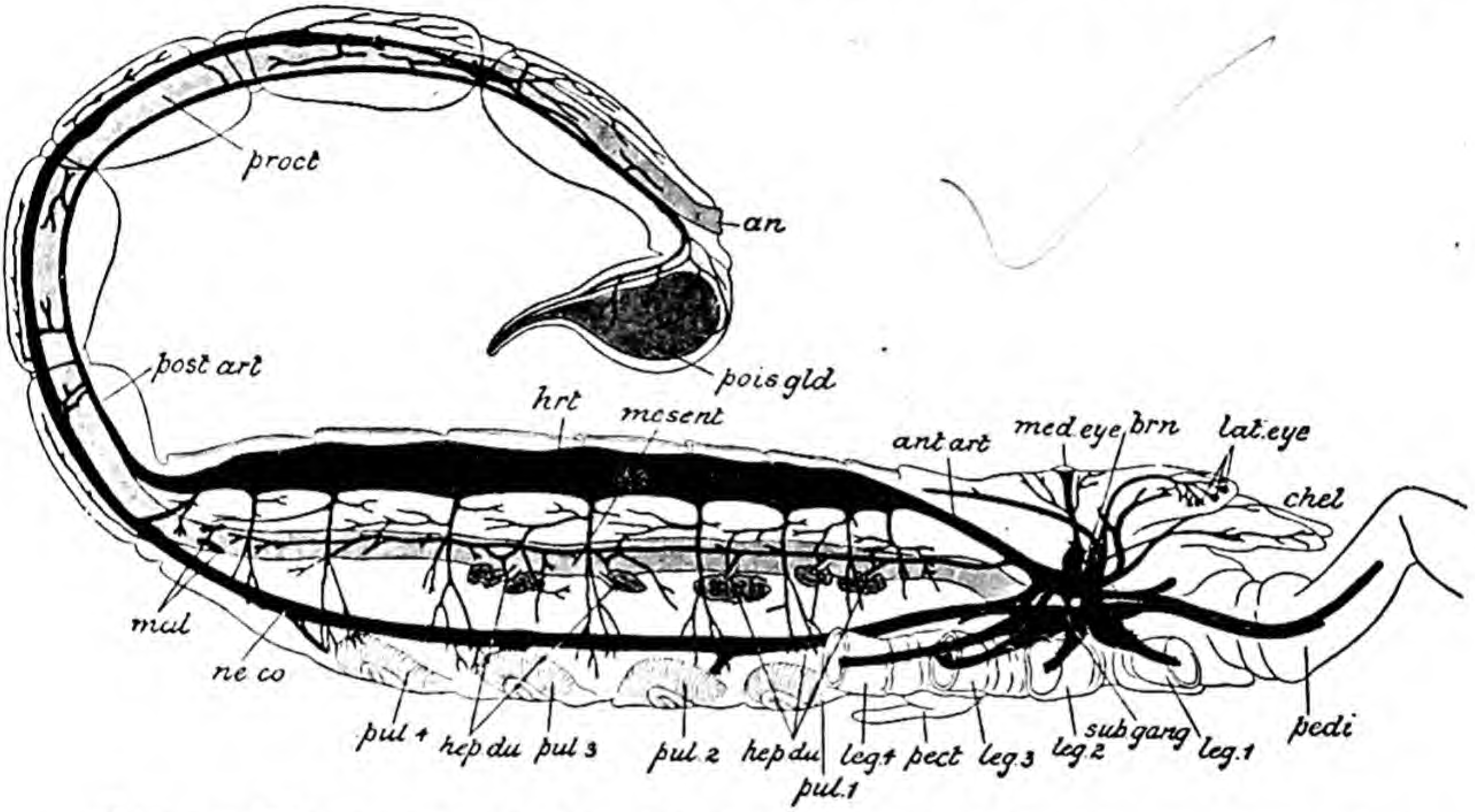


FIG. 490.—Diagrammatic side view of the internal organs of **Scorpion.** *an.* anus; *ant. art.* anterior aorta; *brn.* brain; *chel.* chelicerae; *hep. du.* hepatic duct; *hrt.* heart; *lat. eye,* lateral eyes; *leg 1—4,* legs; *mal.* Malpighian tubes; *med. eye,* median eye; *mesent.* mesenteron; *ne. co.* nerve-cord; *pect.* pectines; *pedi.* pedipalp; *pois. gld.* poison gland; *post. art.* posterior aorta; *proct.* proctodæum; *pul. 1—pul. 4,* pulmonary sacs; *sub. gang.* sub-œsophageal ganglion. (From Leuckart, after Newport and Blanchard.)

numerous narrow spaces between the laminæ the air penetrates, and oxygenates the blood which enters the interior of the laminæ from the ventral sinus.

A pair of *coxal glands* are situated near the base of the third walking leg (Fig. 488, 5) in the fifth segment of the prosoma. The coxal glands are derived from cœlomoducts and are, in the embryo-Scorpion, represented in segments three, four, five, six, and eight (not counting the pre-cheliceral and pre-genital segments) by tubes which grow out from the cœlomic sacs; in the adult Scorpion only the cœlomoducts of segment five persist in the form of the coxal glands which probably function as excretory organs. The cœlomoducts of segment eight form the mesodermal portion of the gonoducts.

The **nervous system** is constructed on a plan which bears a considerable resemblance to that of the Crayfish and that of the Cockroach. There is a bilobed cerebral ganglion or *brain* (Fig. 490, *brn.*) from which nerves are given off to the eyes; a nerve-collar formed of a pair of *œsophageal connectives* unites ventrally in a *sub-œsophageal ganglion*, forming the anterior part of a *ventral nerve-cord* (*ne. co.*). The connectives and sub-œsophageal ganglion give rise to the nerves of the first six pairs of appendages and of the operculum, the pectines, and the two following segments. The first ganglion behind the sub-œsophageal ganglion appears in the fifth segment of the pre-abdomen (not counting the pre-genital segment); behind which a ganglion occurs regularly in each segment as far back as the fourth of the post-abdomen.

The **sense-organs** are the *eyes* and *pectines*. The lateral eyes (Fig. 510) are similar in character to the simple eyes or ocelli of Insects. The two larger central eyes (Fig. 511) differ from them in having the retinal cells arranged in groups as in the compound eye, but resemble them in the presence of a single cuticular lens.

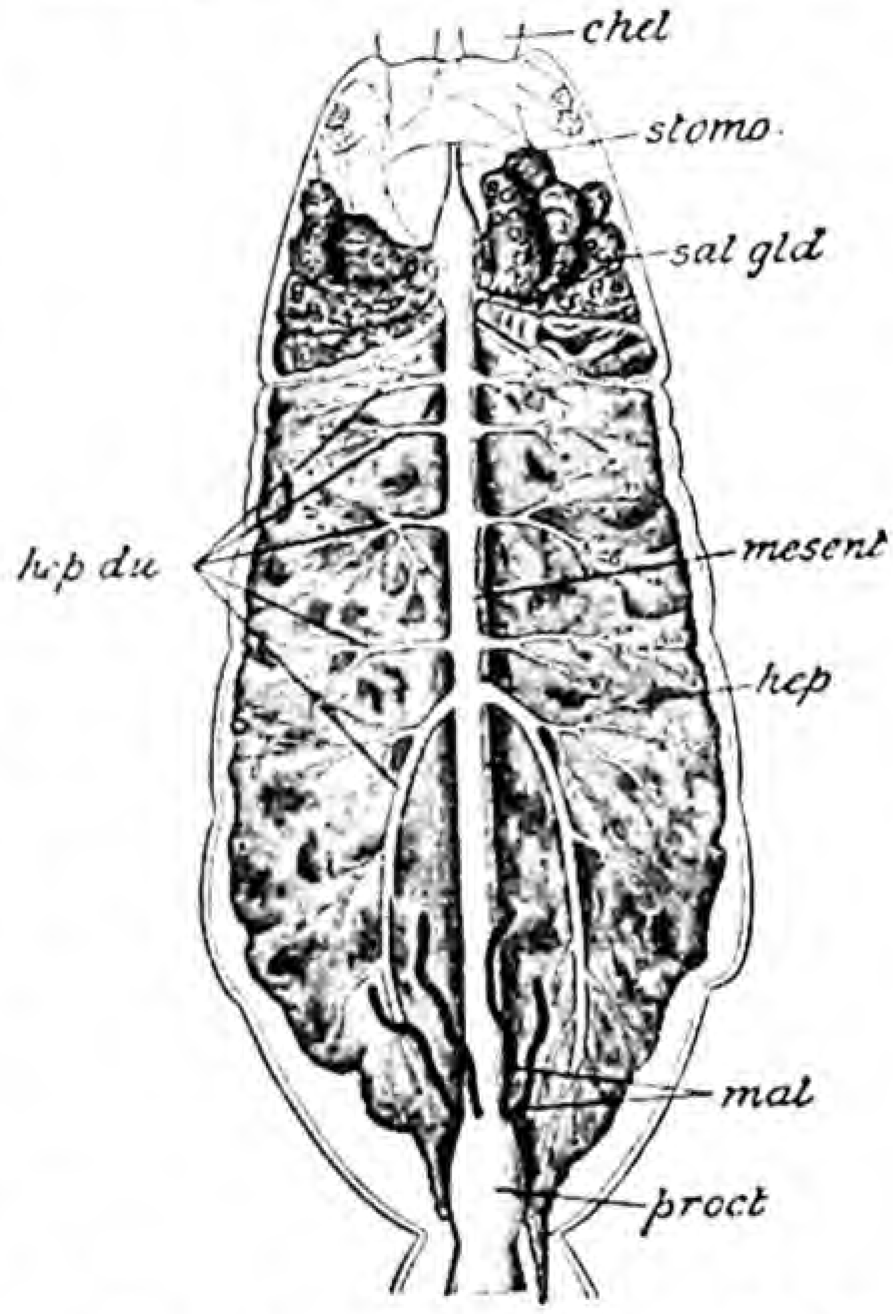


FIG. 491.—Dorsal view of the internal organs of **Scorpion**. *chel.* chelicerae; *hep.* liver; *hep. du.* hepatic ducts; *mal.* Malpighian tubes; *mesent.* mesenteron; *proct.* intestine; *sal. gld.* salivary glands; *stomo.* stomodæum. (From Leuckart, after Blanchard.)

Reproductive organs.—In the male the *testes* consist of two pairs of longitudinal tubules united by cross branches. These are connected with a median *vas deferens*, the terminal portion of which, provided with *accessory glands*, is modified to form a double penis; its external opening is just behind the operculum, as already noticed. There is an unpaired *ovary*, which is made up of three longitudinal tubules with transverse connecting branches; the oviducts open on the operculum.

Scorpions are viviparous. The *eggs*, which are spherical or oval, and in most species contain a large amount of food-yolk, lie in a follicle formed of a diverticulum of the oviduct. Fertilization either occurs in the follicle or after the egg has escaped into the oviduct. The further development takes place in the oviducts; and, when born, the young Scorpion differs from the parent very little save in size.

Development.—The cleavage is of the type to which the term *discoidal* is applied. On one pole are formed a number of cells in the form of a one-layered *disc* or cap, which gradually spreads over the yolk. On this appears a

thickening—the *ventral plate* (Fig. 492) corresponding to that of the Insect. A longitudinal groove which appears on the surface of this may be regarded as representing an elongated blastopore (Fig. 492, *A*). The cells of the blastoderm of the ventral plate become divisible into three layers—*ectoderm, endoderm,* and *mesoderm.* The mesoderm undergoes division into a series of masses which are hollowed out to form the primitive segments (*B*) and their cavities.

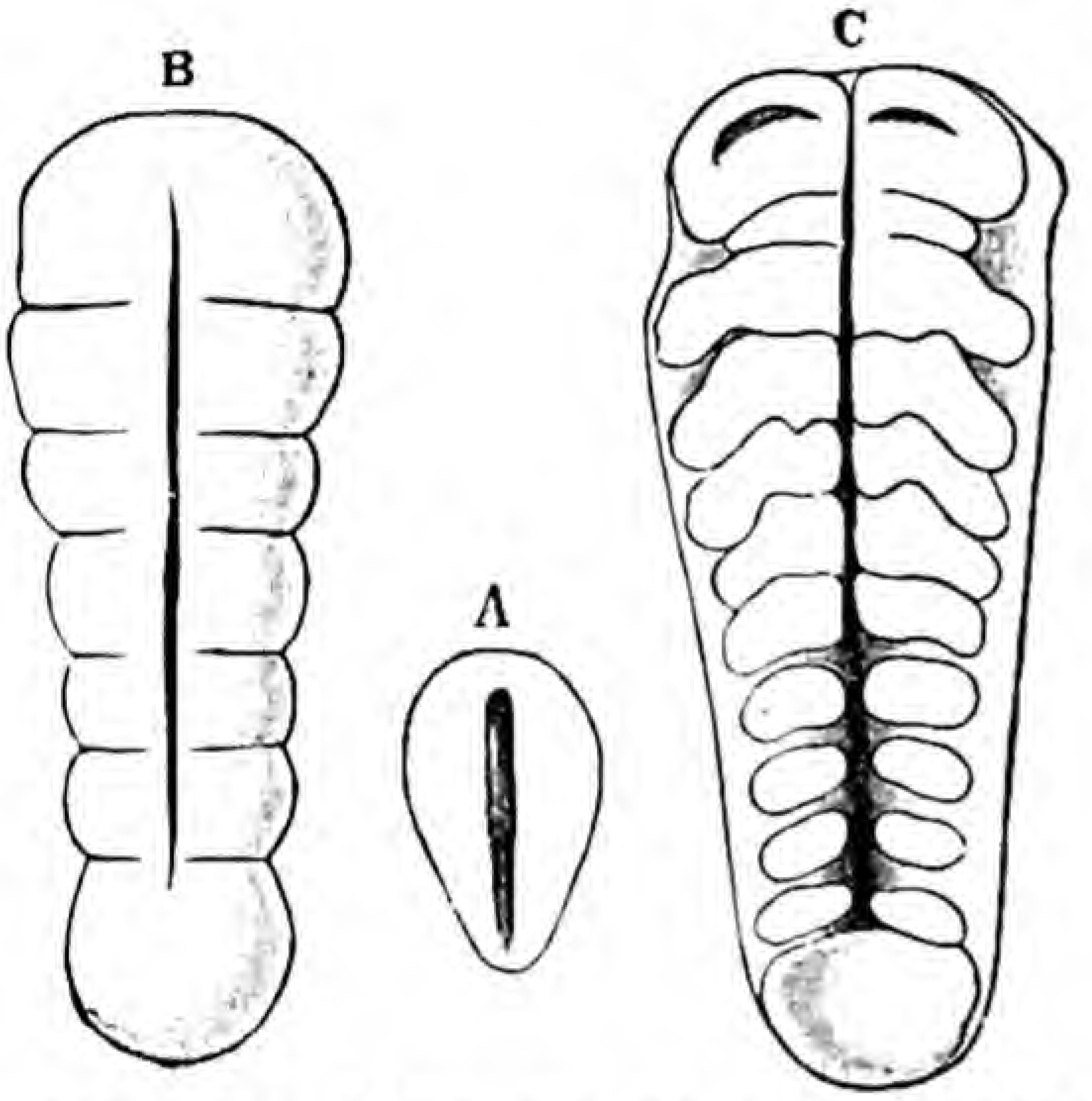


FIG. 492.—Three surface views of the ventral plate of a developing **Scorpion.** *A,* before the appearance of segments; *B,* after five segments have become formed; *C,* after the appendages have begun to be formed. (From Balfour, after Metschnikoff.)

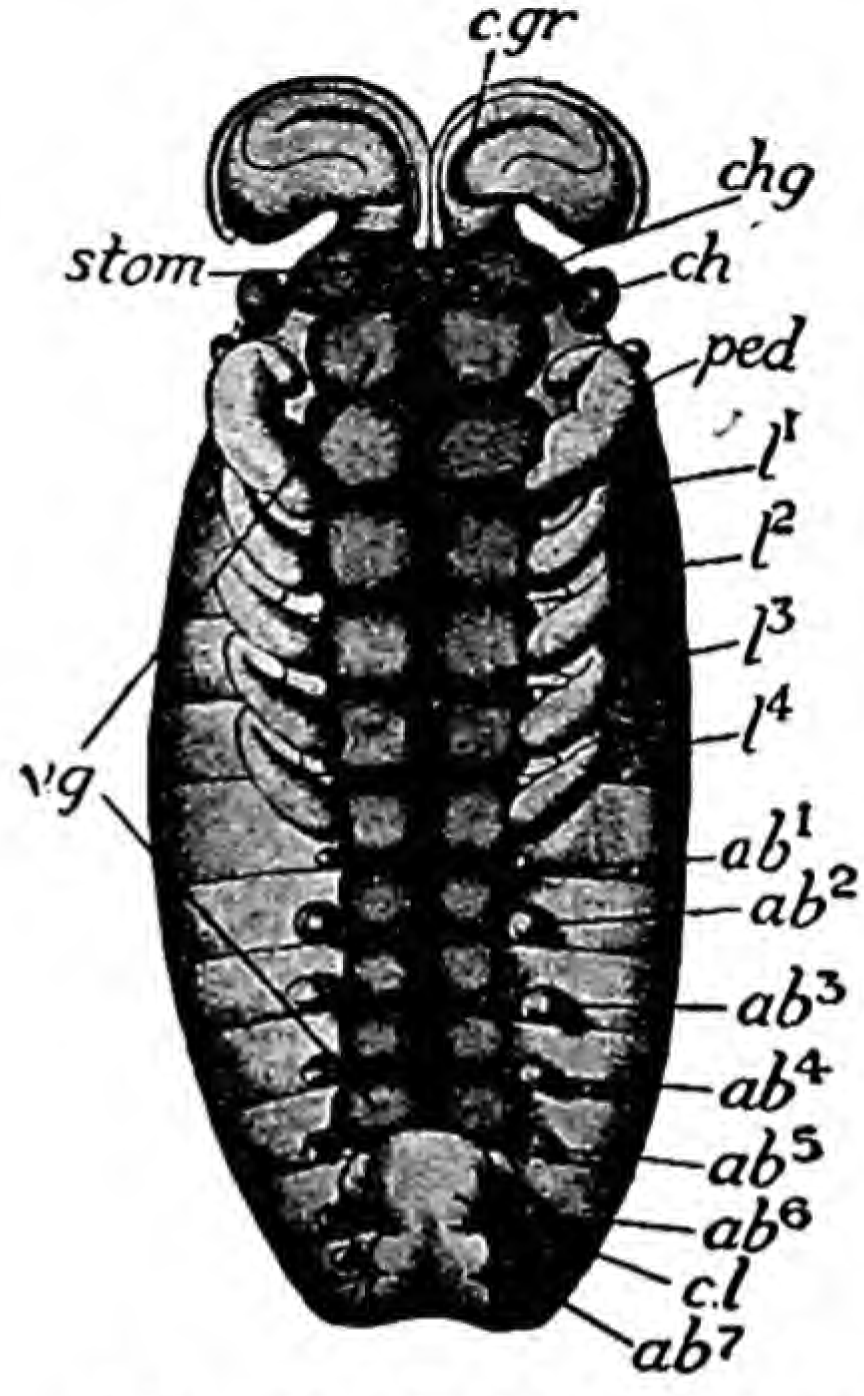


FIG. 493.—Embryo of Scorpion (**Euscorpio carpathicus**), with rudimentary appendages. *ab*$^{1-7}$, abdominal appendages; *ch.* chelicera; *ch. g.* rudiment of cheliceran ganglion; *c. gr.* cephalic groove; *c. l.* caudal lobe; *l*$^{1-4}$, walking legs; *ped.* pedipalp; *stom.* opening of stomodæum; *v. g.* ganglia of ventral nerve cord. (From MacBride, after Brauer.)

Embryonic membranes—*serosa* and *amnion*—are formed as in the Insects. When about ten segments have become distinguishable, the rudiments of appendages (Fig. 502, *C*, and Fig. 503) appear in the form of hollow processes of the segments on either side of the middle line. Behind the rudiments of the thoracic limbs appear a series of seven pairs of abdominal appendages (*ab*$^{1-7}$); the first (pre-genital) disappears early; the place of the second is afterwards taken by the operculum; the third develops into the pectines. The four posterior pairs become aborted; the book-lungs appear as pits at their bases.

2. Distinctive Characters and Classification.

The Arachnida are air-breathing Arthropoda in which the body is usually distinguishable into two regions—cephalothorax and abdomen. The cephalothorax bears sessile, usually simple eyes, two pairs of jointed appendages—the cheliceræ and pedipalpi—and four pairs of legs. There are no antennæ. The organs of respiration, when present, are usually either tracheæ or book-lungs, but in the Xiphosura take the form of book-gills. Heart and vascular system are usually present; the heart is tubular, like that of the Insects. The sexes are nearly always separate, and there is usually no metamorphosis.

The class is divided into the following orders:—

Order 1.—Eurypterida.

Arachnida with a relatively small cephalothorax, followed by twelve free segments and a terminal, elongated, narrow telson. There are a pair of preoral leg-like or chelate appendages and five more appendages on the cephalothorax, four of which are leg-like. There are pairs of lamellate appendages on certain of the anterior free segments. The exo-skeleton is characteristically sculptured.

This order includes only a number of extinct (Palæozoic) forms of large size (*Eurypterus*, Fig. 494).

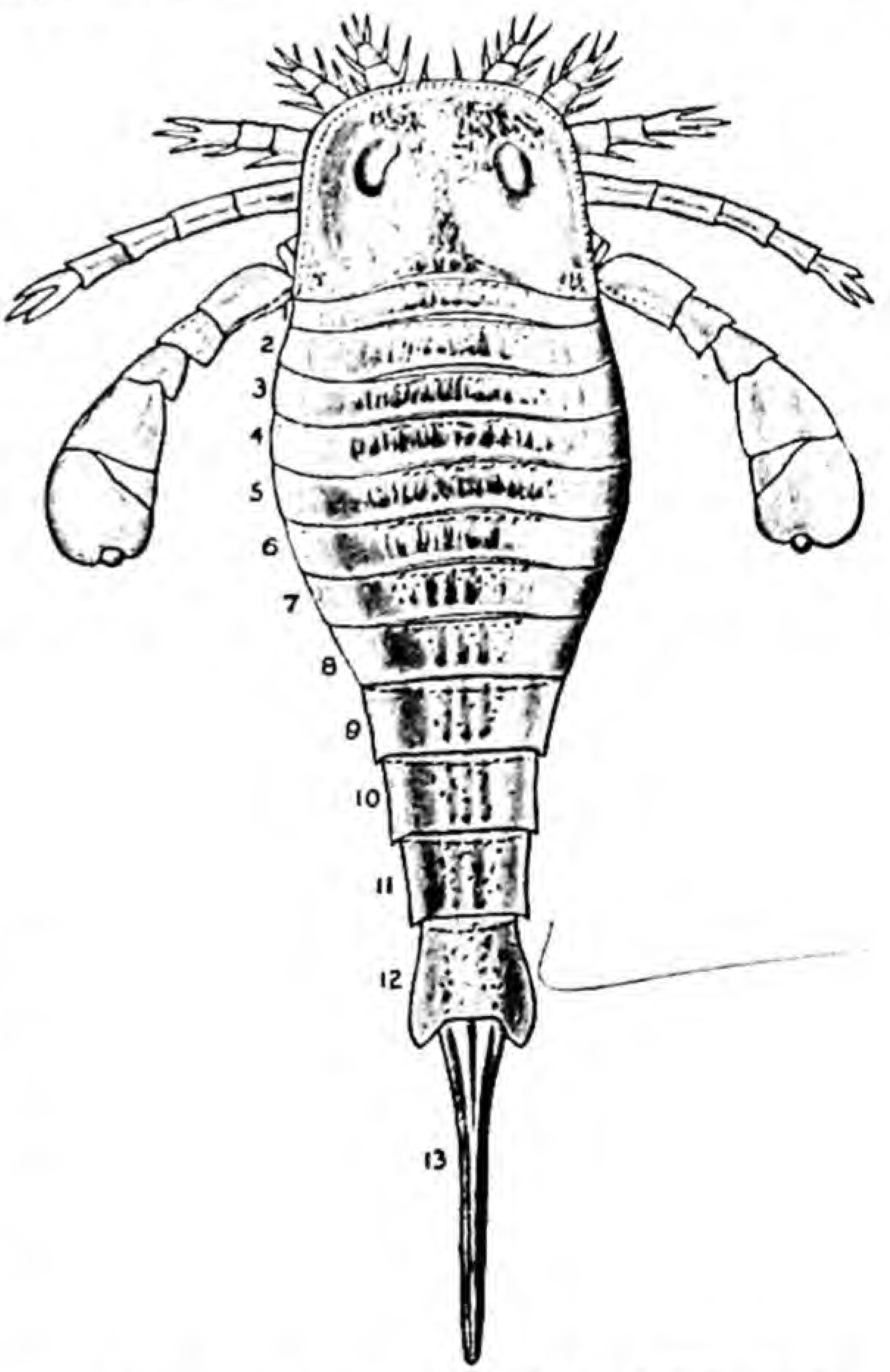


Fig. 494.—**Eurypterus fischeri** (Silurian). (From Nicholson and Lydekker.)

Order 2.—Xiphosura.

Arachnida in which the body consists of a cephalothorax covered over by a broad carapace, and an abdomen consisting of six mesosomatic segments and a vestigal unsegmented metasoma, with a long narrow tail-piece or telson. The cephalothorax bears a pair of short chelate appendages and five pairs of legs. The abdomen bears in front a pair of united plate-like appendages, forming the *operculum*, followed by five pairs of flat appendages over

lapped by the operculum. The organs of respiration are lamelliform gills attached to the abdominal appendages.

This order includes the King-crabs (*Limulus*, Fig. 495).

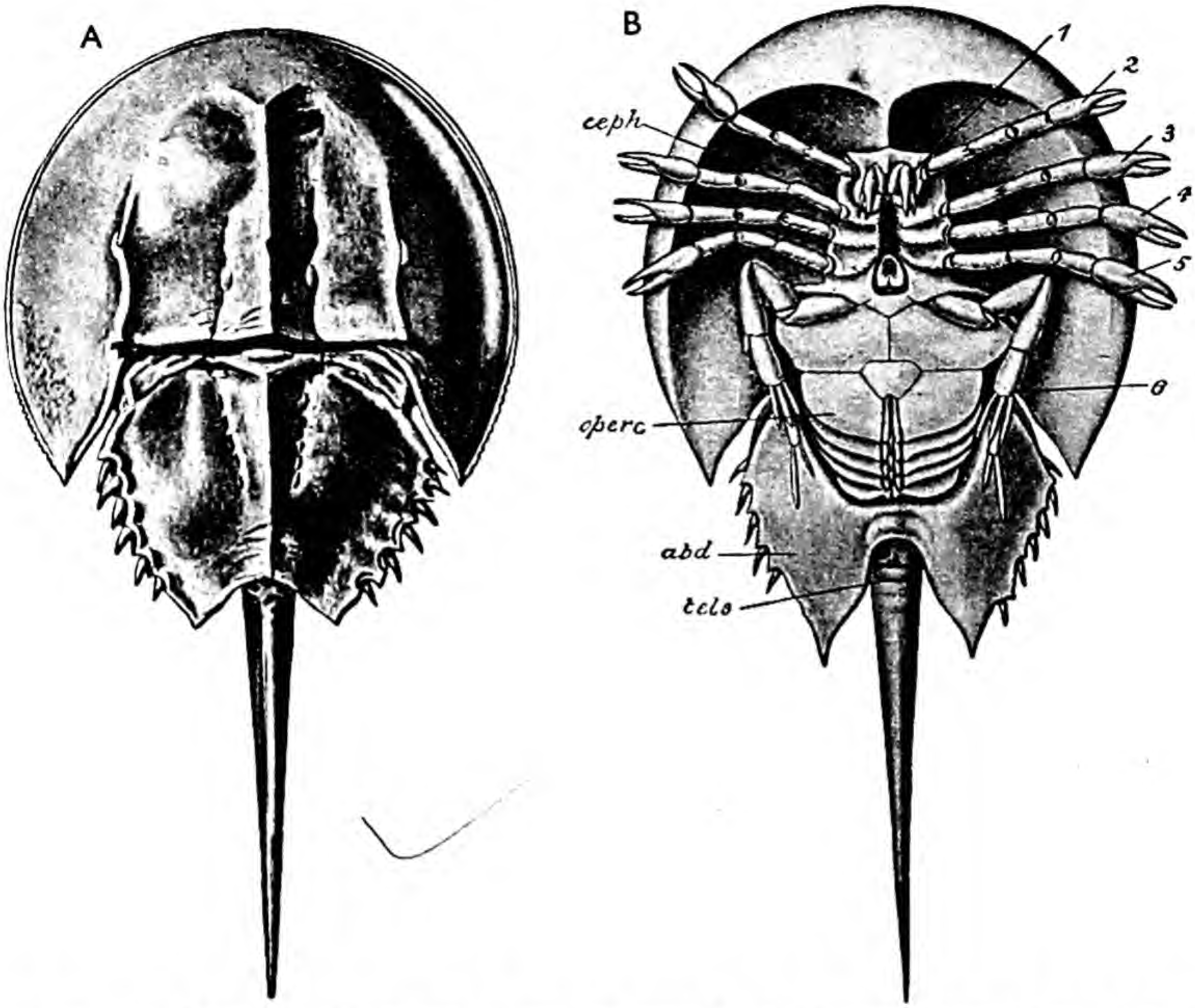


FIG. 495.—**Limulus.** *A*, dorsal, *B*, ventral aspect; *1—6*, appendages of cephalothorax; *abd.* abdomen; *ceph.* cephalothorax; *operc.* operculum, behind which are seen the series of abdominal appendages; *tels.* caudal spine or telson. (After Leuckart.)

ORDER 3.—SCORPIONIDEA.

Arachnida in which the body consists of a continuous cephalothorax and an abdomen, the latter consisting of an anterior broader pre-abdomen of seven segments, and a posterior, narrower post-abdomen of five segments, with a caudal spine in the form of a sting. There are small chelate cheliceræ and large chelate pedipalpi. A pair of comb-like pectines occur on the second segment of the pre-abdomen. The organs of respiration are four pairs of book-lungs in the third, fourth, fifth and sixth segments of the pre-abdomen.

This order includes the Scorpions (*Scorpio*, Fig. 488).

ORDER 4.—PEDIPALPIDA.

Arachnida in which the body consists of a generally unsegmented cephalothorax and a flattened abdomen of nine to twelve segments joined to the cephalothorax by a narrow neck (*pedicle*). The cheliceræ are simple, the

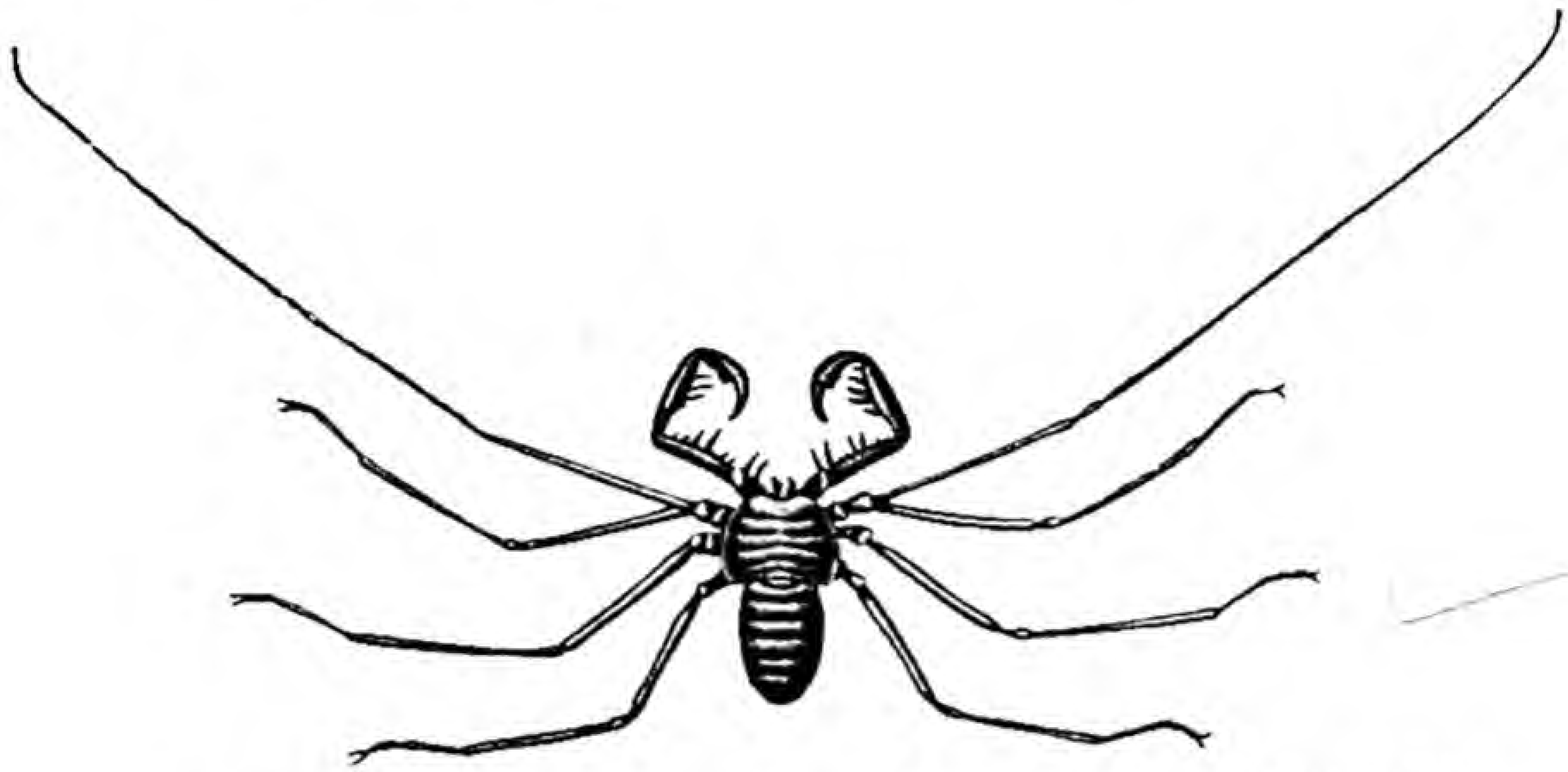


FIG. 496.—**Phrynichus.** (From Cuvier's *Animal Kingdom.*)

pedipalpi simple or chelate, and the first pair of legs terminate in a many-jointed flagellum. The organs of respiration are two pairs of book-lungs on the second and third segments of the abdomen.

This order includes the Scorpion-spiders (*Phrynichus*, Fig. 496).

ORDER 5.—ARANEIDA.

Arachnida in which the body is composed of an undivided cephalothorax and a usually unsegmented abdomen, which is generally soft and rounded, and attached to the cephalothorax by a narrow pedicle. The cheliceræ are subchelate, with poison-glands; the pedipalpi simple. The organs of respiration are book-lungs alone, or book-lungs combined with tracheæ.

This order comprises all the true Spiders (*Aranea*, Fig. 497).

FIG. 497.—Spider (**Aranea diademata**).

ORDER 6.—PALPIGRADI.

Small Arachnida in which the last two cephalothorax segments are free; the abdomen consists of ten segments and is joined to the cephalothorax by a

pedicle; the telson has the form of a long jointed *flagellum*. The chelicerae are chelate, the pedipalpi leg-like. The organs of respiration are three pairs of book-lungs.

This order includes *Kœnenia* (Fig. 498).

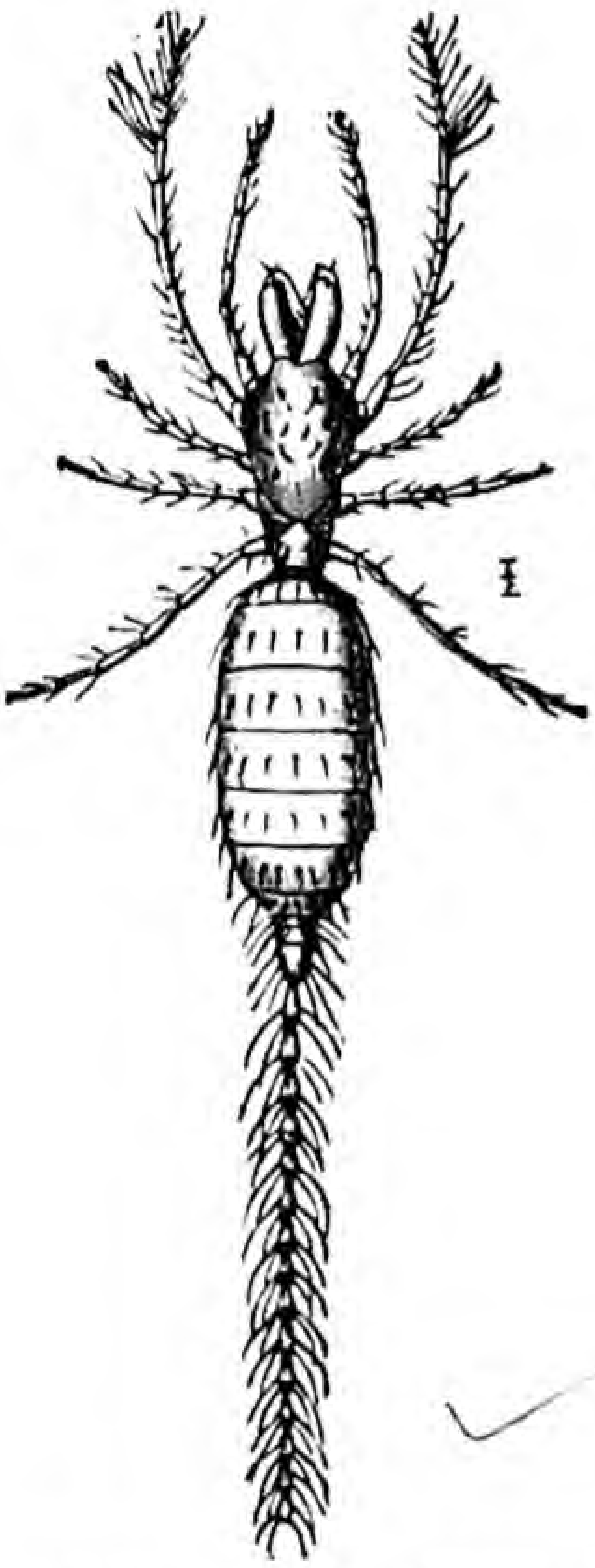


FIG. 498.—**Kœnenia mirabilis**, much enlarged. (From *The Cambridge Natural History* (Macmillan & Co., Ltd.), after Hansen.)

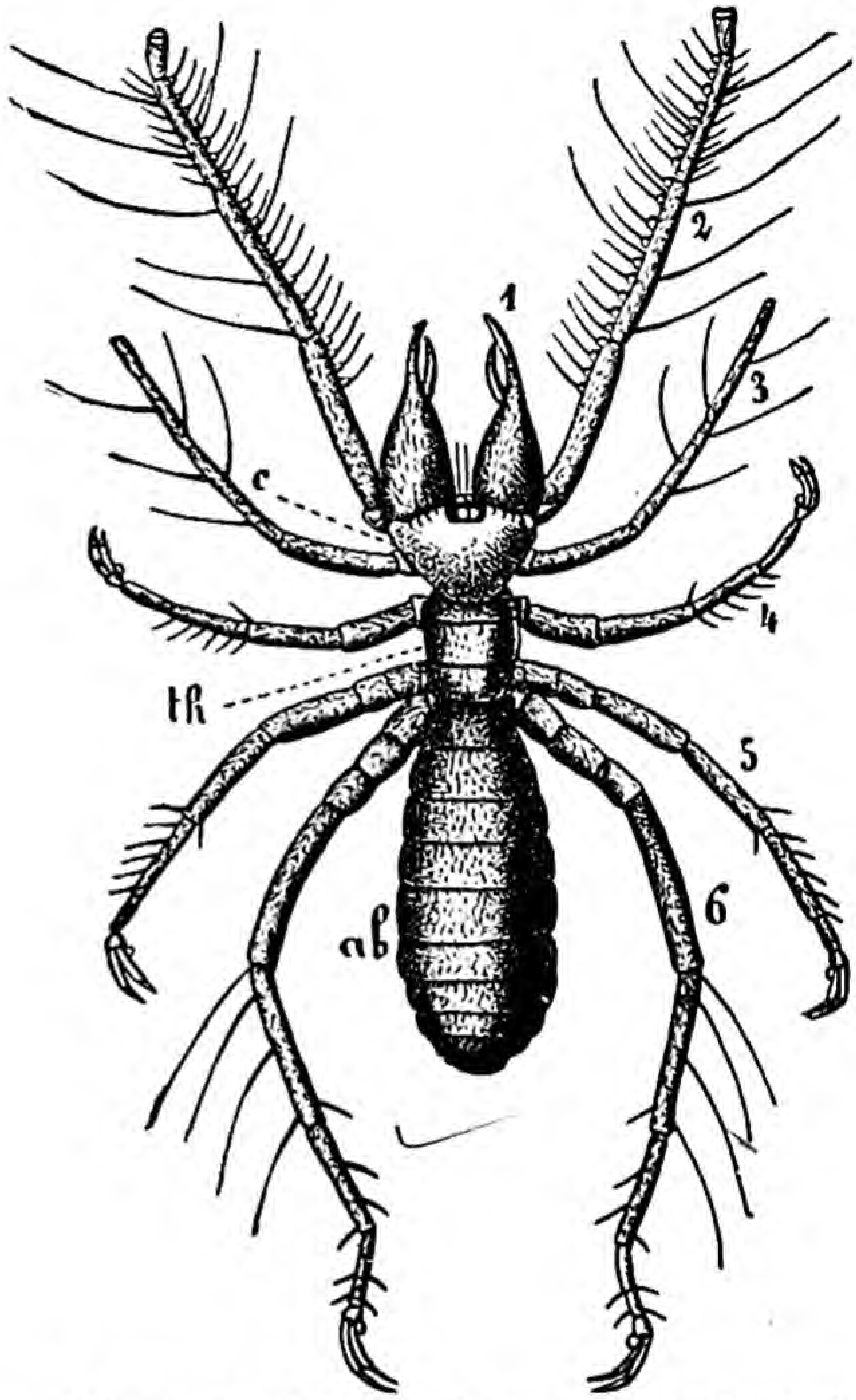


FIG. 499.—**Galeodes dastuguei** ♀, natural size. *1*—*6*, the six pairs of appendages; *1*, chelicerae; *2*, pedipalpi; *c*. head; *th*. thorax; *ab*. abdomen. (From Lang, after Dufour.)

ORDER 7.—SOLIFUGÆ.

Arachnida with three regions—"head," "thorax" (of three segments), and abdomen (of ten segments). The chelicerae are chelate; the pedipalpi elongated and leg-like. The organs of respiration are tracheæ.

This order includes *Galeodes* (Fig. 499).

ORDER 8.—PSEUDOSCORPIONIDEA (CHELONETHI).

Arachnida in which there is a continuous cephalothorax, sometimes marked dorsally with two transverse grooves, and a broad abdomen of twelve segments, not divided into pre- and post-abdomen, and not provided with a sting. The cheliceræ are very small, the pedipalpi similar to those of the Scorpions. The organs of respiration are a system of tracheæ. A pair of spinning glands are present.

This order includes the Book-scorpions (*Chelifer*, Fig. 500).

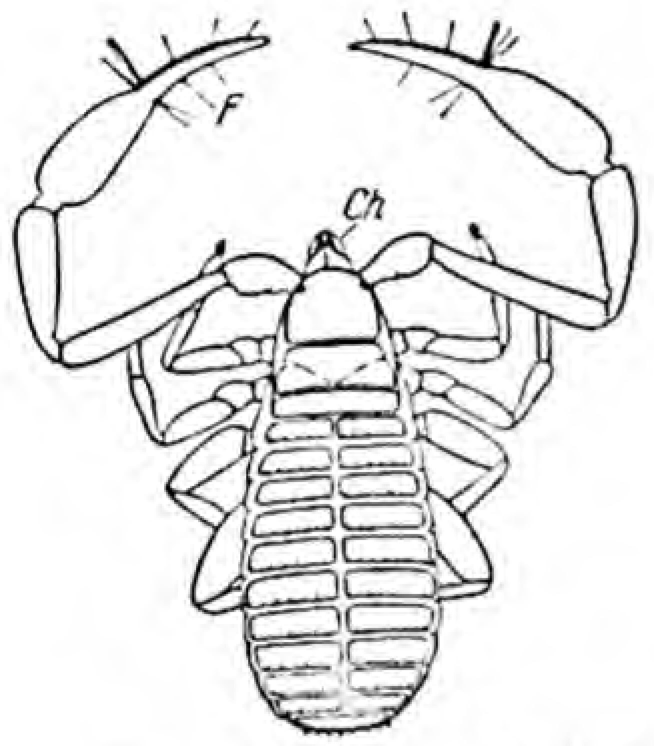


FIG. 500.—**Chelifer cancroides.** *Ch.* cheliceræ; *F.* pedipalpi. (From Claus, Grobben, and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after M. Beier.)

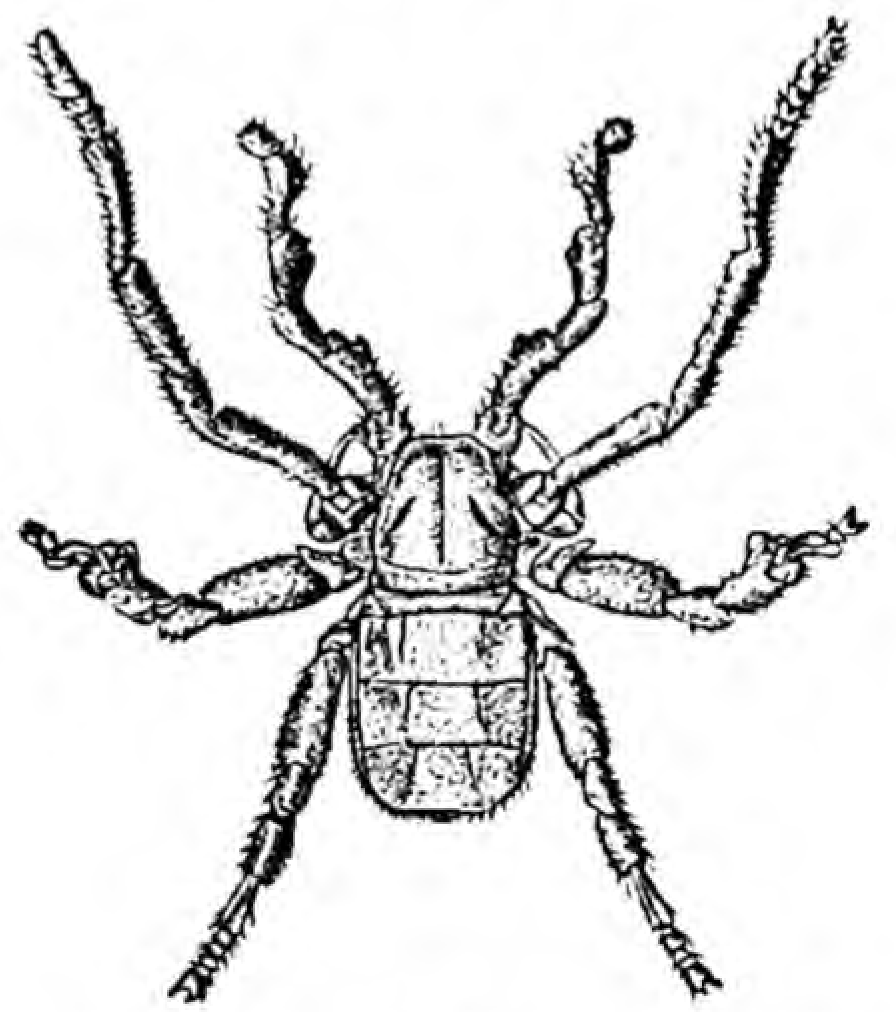


FIG. 501.—**Cryptocellus simonis.** (From *The Cambridge Natural History* (Macmillan & Co., Ltd.), after Hansen and Sörensen.)

ORDER 9.—RICINULEI.

Arachnida with a continuous cephalothorax with a movable anterior projection, called cucullus; the abdomen is joined to the cephalothorax by a pedicle and consists apparently of four, really of nine segments. The cheliceræ and the pedipalpi are chelate. The organs of respiration are tracheæ.

This order includes *Cryptocellus* (Fig. 501).

ORDER 10.—PHALANGIDA (OPILIONIDEA).

Arachnida with an unsegmented cephalothorax, and an abdomen of ten segments, continuous with the cephalothorax. The cheliceræ are chelate, the

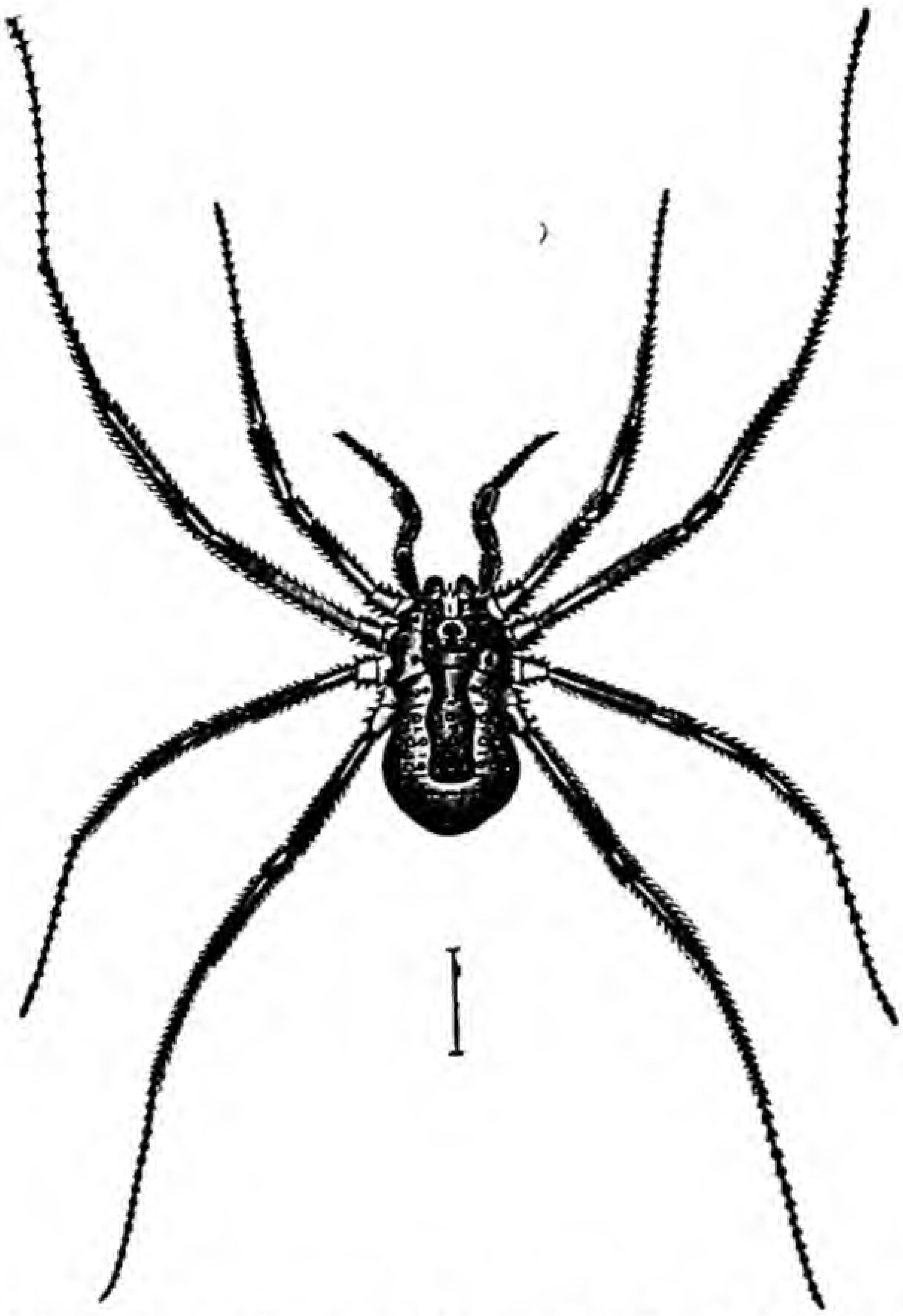


FIG. 502.—**Oligolophus spinosus.** (From *The Cambridge Natural History* (Macmillan & Co., Ltd.), after Pickard-Cambridge.)

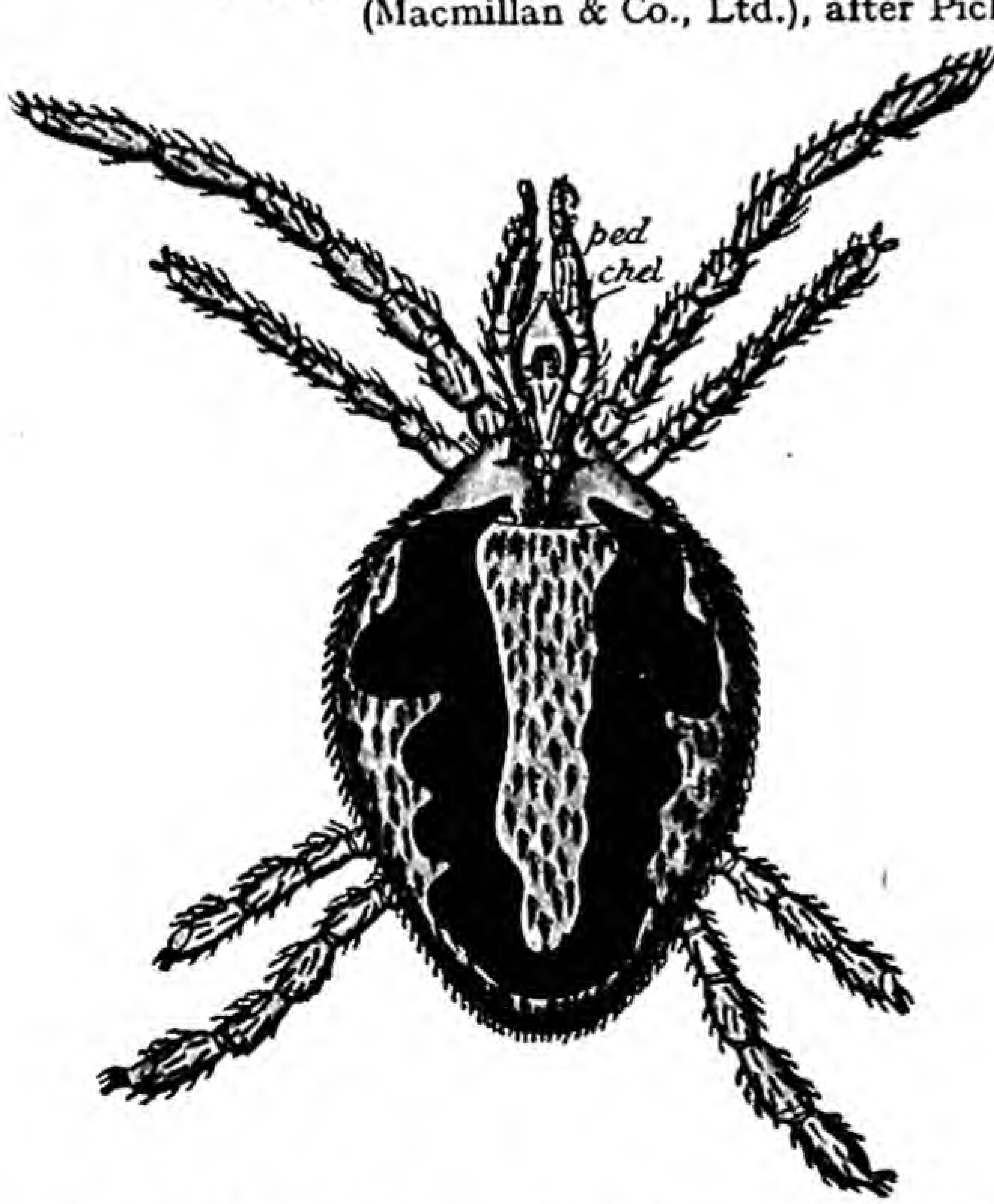


FIG. 503.—Water mite (**Trombidium fuliginosum**), female. *chel.* chelicerae; *ped.* pedipalpi. (After Leuckart.

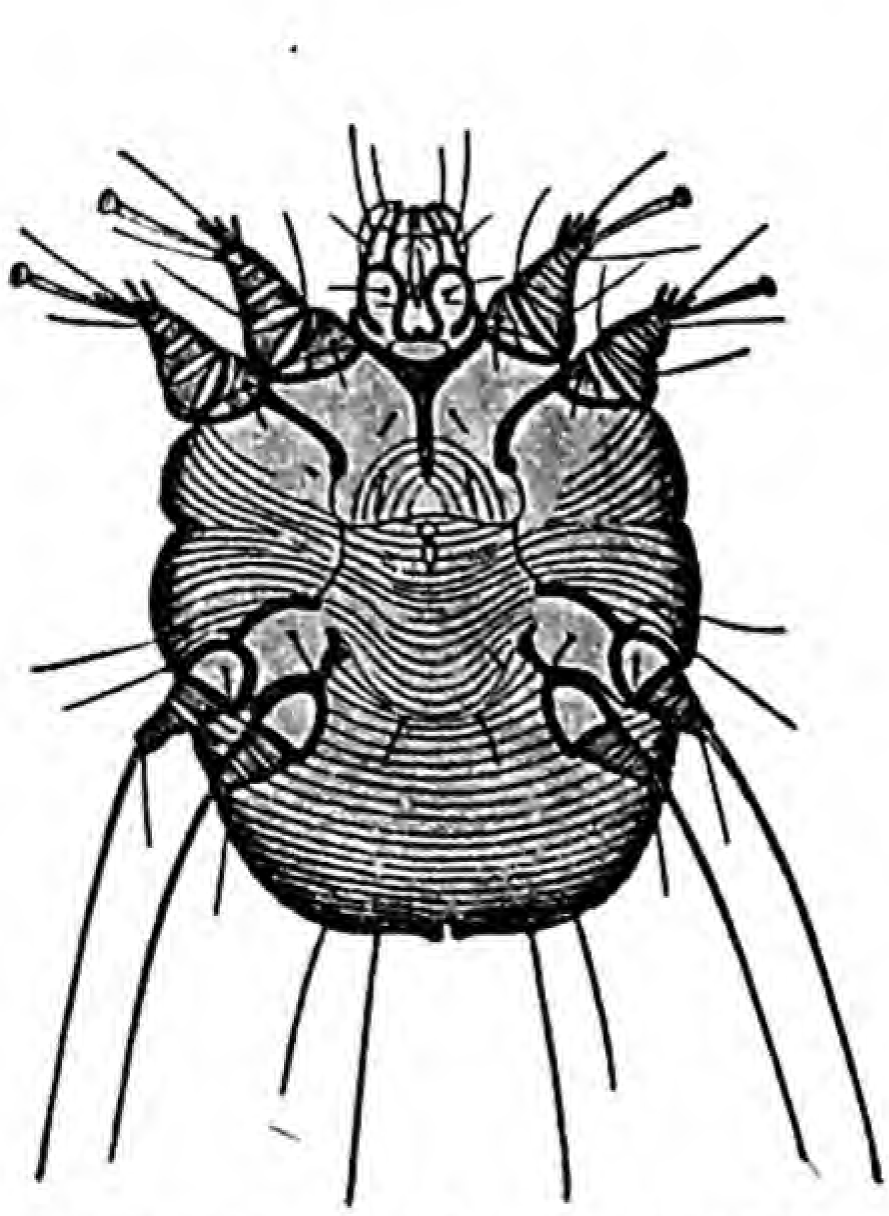


FIG. 504.—Itch mite (**Sarcoptes scabiei**). (After Leuckart.)

pedipalpi leg-like. The organs of respiration are tracheæ. No spinning glands are developed.

This order includes the Harvestmen (*Oligolophus*, Fig. 502).

ORDER II.—ACARINA.

Arachnida in which the body exhibits no visible division into regions. The mouth-parts are adapted either for biting or piercing and sucking. The organs of respiration, when present, are in the form of tracheæ.

This order includes the Mites (Figs. 503 and 504), and the Ticks.

3. GENERAL ORGANIZATION.

The **external form** of the various Arachnida has already been sufficiently described.

Appendages.—In the *Eurypterida* (Fig. 494) there are usually five pairs of limbs surrounding the mouth and, with the exception of the first, toothed at the bases in order to perform the functions of jaws; the last pair are stouter than the others and are expanded so as, apparently, to assume the character of swimming paddles. Certain of the more anterior of the free segments bear paired lamelliform appendages which probably carried the branchiæ, as in the Xiphosura.

In the *Xiphosura* or King-crabs (Fig. 495), the anterior appendages resemble those of the Scorpion. In front of the mouth is a pair of short, three-jointed, chelate appendages, the *cheliceræ* (1), at the sides of a labrum (*rostrum*) or upper lip. Behind these follow a series of five pairs of legs, the bases of all of which, with the exception of the last, are covered with spines, and have the action of jaws, while the extremities are for the most part chelate. The first pair of appendages of the abdomen are flat plates, which are united together in the middle line and together form the broad *operculum* (*operc.*) overlapping all the posterior appendages; on its posterior face are the two genital apertures. The posterior appendages, of which there are five pairs, are thin flat plates to which the gills are attached; each of them is divided by a suture into a small inner ramus or endopodite, and a larger external ramus or exopodite. Between the sixth pair of appendages is a pair of processes, the *chilaria*.

In the *Pedipalpi*, or Scorpion-spiders (Fig. 496), the cheliceræ end in simple claws; they are probably provided with poison-glands; the pedipalps are very long, either clawlike or chelate; the first pair of legs are very long and slender, their terminal part made up like antennæ of numerous short joints. There are eight eyes on the carapace, two larger central, and six smaller marginal.

In the *Spiders* (Fig. 497) the abdomen is rounded, unsegmented, and separated off from the cephalothorax by a constriction. The cheliceræ are sub-chelate, and the duct of a large poison-gland opens at the extremity. The

pedipalpi are elongated, six-jointed, and end in simple extremities; in the male (Fig. 512) the terminal joint is modified to serve for the reception and transference of the sperms. At the extremity of the abdomen is the spinning apparatus or *arachnidium* (Fig. 506, *arach.*). This consists of four or six elevations, the *spinnerets*, usually jointed, probably derived from embryonic rudiments of abdominal appendages. On the surfaces of these open the numerous fine ducts of the spinning glands (*sp. glds.*), secreting the material of which the spider's web is composed. The fine threads of viscid secretion issuing from the ducts harden on exposure to the air, and are worked up into the web by means of the posterior legs.

In the *Acarina* or Mites and Ticks (Figs. 503 and 504), the form of the mouth-parts varies somewhat in the different families. Sometimes the basal

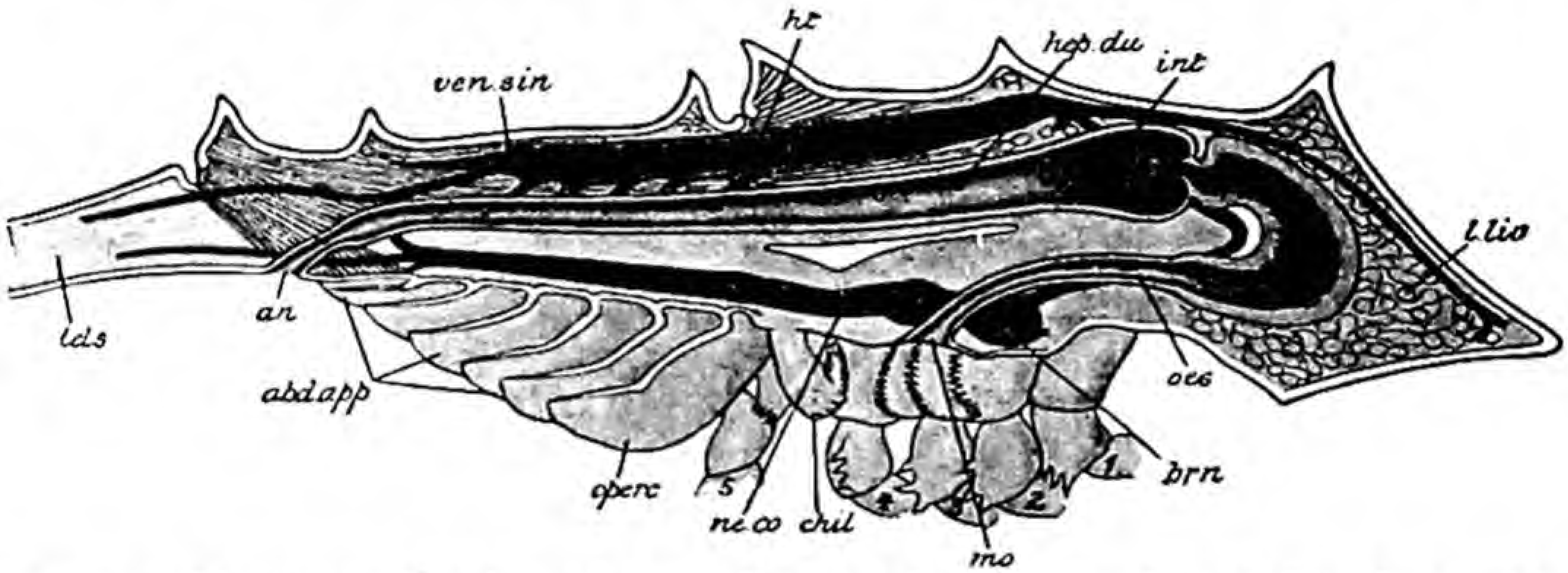


FIG. 505.—Diagrammatic view of a median longitudinal section of **Limulus.** *abd. app.* abdominal appendages; *an.* anus; *brn.* brain; *chil.* chilaria; *hep. du.* opening of one of the hepatic ducts; *ht.* heart; *int.* intestine; *l. liv.* "liver"; *mo.* mouth; *ne. co.* nerve-cord; *œs.* œsophagus; *operc.* operculum; *tels.* telson; *ven. sinus,* venous sinus; *1—5,* legs. (From Leuckart, partly after Packard.)

portions of the pedipalpi form a sucking proboscis enclosing the stylet-like chelicerae, modified to form piercing organs; sometimes these appendages are claw-like or chelate. The legs vary somewhat in shape in the different groups, according as they are used for prehension, for creeping, for running, or for swimming; they end usually in two claws, between which there may be discs or stalked suckers.

Internal skeleton.—A cartilaginous internal **endosternite** of the same nature as that which has been described as occurring in the Scorpions is found in Limulus and in certain Spiders, but not in the other groups.

Coxal glands, similar to those that have been described in the Scorpion, occur also in the Xiphosura, in most Spiders, in the Solifugæ and Phalangida, and in some Acarina.

Alimentary system.—In the Xiphosura, the mouth (Fig. 505, *mo.*), which is situated some distance behind the anterior extremity of the body, leads into a suctorial pharynx, followed by a stomach, which opens into the elongated

mesenteron; the proctodæum, a short tube with folded walls, opens on the exterior at the posterior extremity of the abdomen. Into the mesenteron, as in the Scorpion, open the ducts of a large gland, usually termed the "liver" (*l. liv.*).

The mouth of the Spiders leads into a pharynx (Fig. 506, *ph.*) followed by a narrow œsophagus (*œs.*) expanded behind into a special *sucking stomach* (*suck. st.*). The *mesenteron* (*mesent.*) gives off in the cephalothorax a pair of large diverticula from each of which arise five narrow branches (*cæc.*), the last four of which enter the bases of the legs; in the abdomen it is surrounded by a

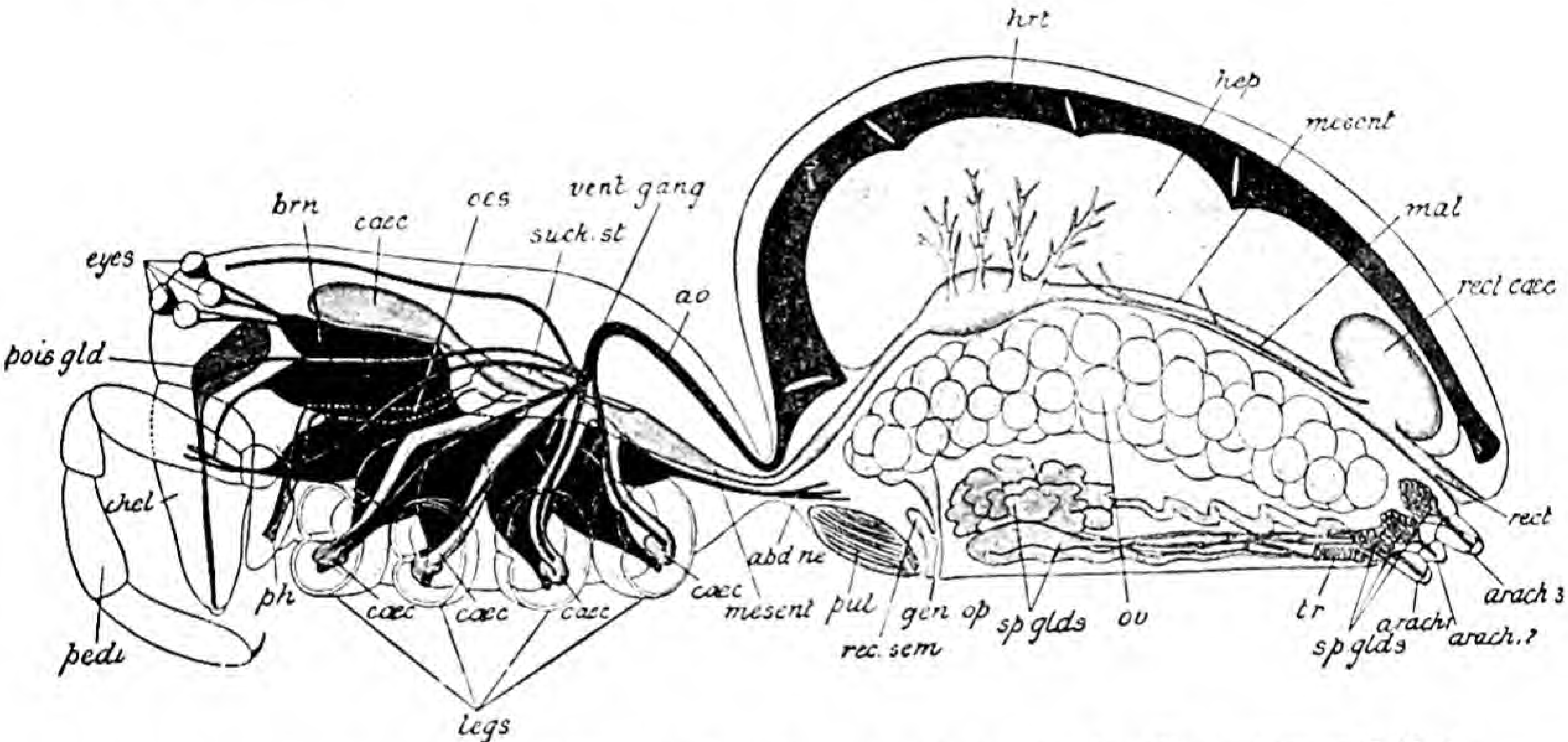


FIG. 506.—Diagrammatic lateral view of the internal organs of a dipneumonous **Spider.** *abd. ne.* abdominal nerves; *ao.* aorta; *arach 1, 2, 3.* arachnidium; *brn.* brain; *chel.* cheliceræ; *cæc.* mesenteric diverticula and their branches; *gen. op.* genital opening; *hep.* "liver"; *hrt.* heart; *legs*, legs; *mal.* Malpighian tubes; *mesent.* mesenteron; *oes.* œsophagus; *ov.* ovary; *pedi.* pedipalpi; *ph.* pharynx; *pois. gld.* poison gland; *pul.* lung; *rec. sem.* receptaculum seminis; *rect. cæc.* dilatation of the rectum; *rect.* rectum; *sp. glds.* spinning glands; *suck. st.* sucking stomach; *tr.* trachea; *vent. gang.* ventral ganglia of cephalothorax. (After Leuckart.)

mass of cells commonly termed "liver" (*hep.*), the ducts of which open into it. The *rectum* or *proctodæum* gives off dorsally a large *cloacal-sac* (*rect. cæc.*) into which open a pair of narrow tubes, the so-called "Malpighian tubes," which are not the homologues of the tubes so named in the Insects, being, with the cloacal sac, of endodermal and not ectodermal derivation.

In the Pseudoscorpionidea the mesenteron, which is bent into a loop, gives off three diverticula; the proctodæum has also a diverticulum. In the Solifugæ the mesenteron also gives off diverticula; the occurrence of Malpighian tubes is doubtful. In the Acarina there are always diverticula, the number and arrangement of which vary, connected with the mesenteron. There are usually two long Malpighian tubes which may be fused mesially.

A **heart** is absent in many of the Mites. In the other Arachnida a heart is present and has the same general form as in the Scorpions, though always more concentrated.

In the various orders the **organs of respiration** differ a good deal in their character. In the Xiphosura the organs of respiration are external appendages or *gills* (*book-gills*) in the shape of delicate laminæ attached to the abdominal appendages (Fig. 507). In the Pedipalpida there are two pulmonary sacs or book-lungs similar to those of the Scorpions. In the Spiders there are either four pulmonary sacs (Fig. 508) or two pulmonary sacs and a system of tracheæ (Fig. 509). In the Solifugæ and the Pseudoscorpionidea there is a system of tracheæ. Tracheæ are also present in the Phalangida and also in the majority of the Acarina.

The **nervous system** is, in most instances, more concentrated than in the

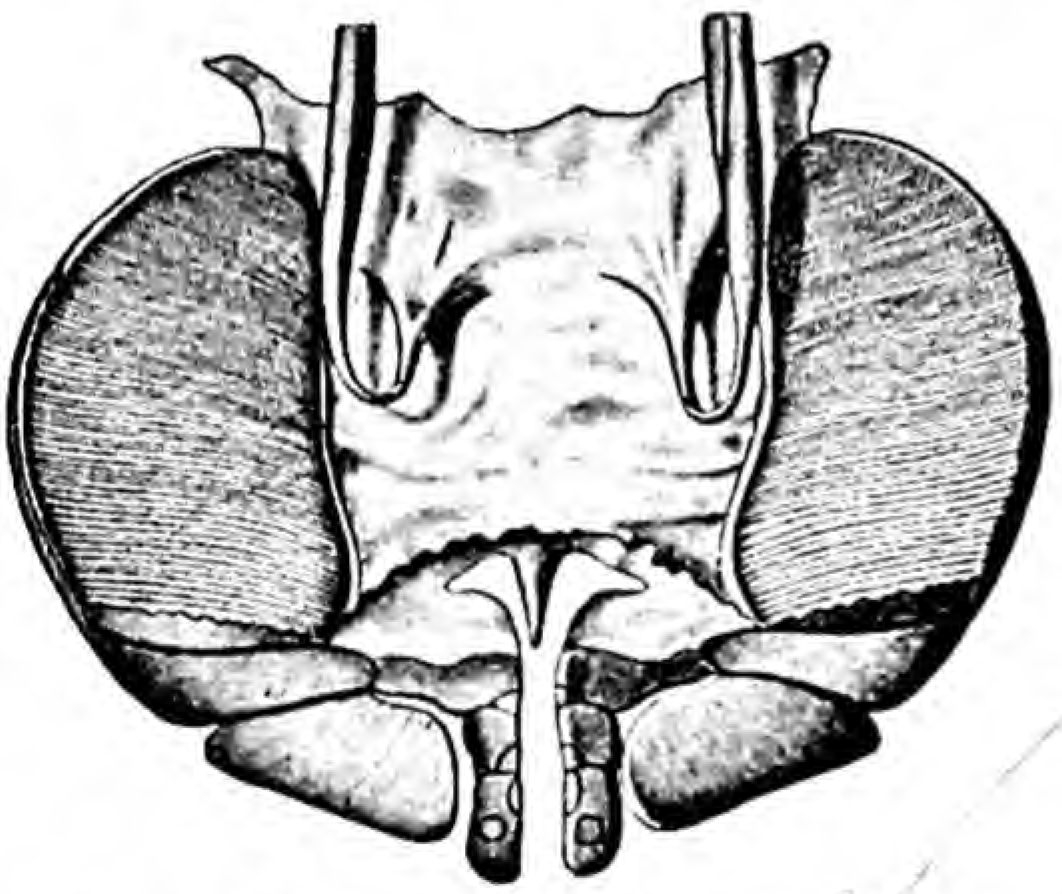


FIG. 507.—One of the book-gills of **Limulus**, with the appendage to which it is attached. (After Lankester.)

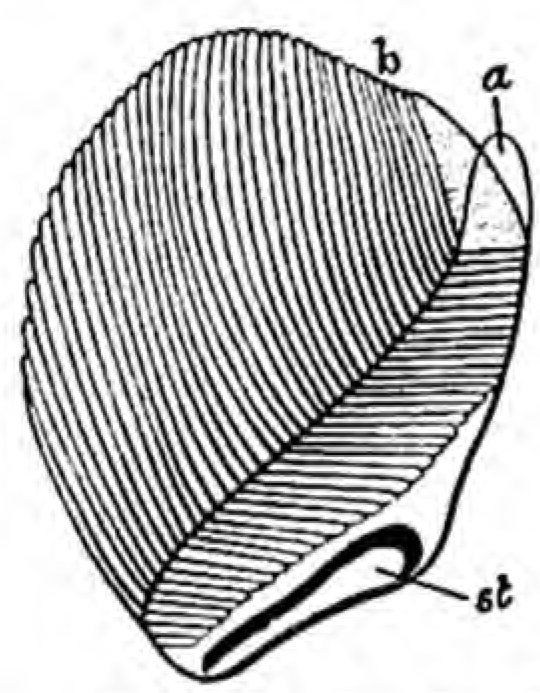


FIG. 508.—Book-lung of a Spider (**Zilla callophylla**). *a*, axis; *b*, laminæ; *st*. stigma. (From Hertwig.)

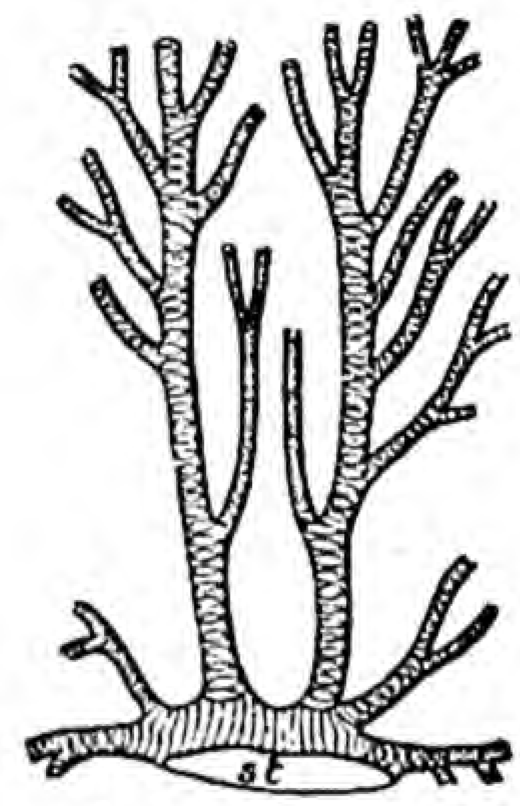


FIG. 509.—Main branches of the tracheal system of a **Spider**. *st*. stigma. (From Hertwig, after Bertkau.)

Scorpions. There may be one or two separate abdominal ganglia behind the mass formed by the united cephalothoracic and anterior abdominal ganglia (Pedipalpida, some Araneida, Solifugæ, Pseudoscorpionidea, and Phalangida). In most of the *Araneida* and in the Acarina all the abdominal are united with all the cephalothoracic ganglia to form a single mass perforated by the œsophagus, the part lying behind, which is much the larger, representing the ventral nerve-cord.

Sense-organs.—In the Eurypterida the cephalothorax bears a pair of large eyes and a pair of ocelli. Similarly the carapace of Limulus bears two large compound eyes and two smaller simple eyes. In the Scorpionidea there are a pair of large eyes about the middle of the carapace and several pairs of smaller eyes on its antero-lateral margin. In the Pedipalpida the carapace bears eight eyes, two larger central and six smaller marginal. The carapace of the Spiders bears six or eight simple eyes whose varying mode of arrangement is

of systematic importance. In the Pseudoscorpionidea and in the Acarina there are two or four eyes, or eyes may be entirely absent. In the Solifugæ and Phalangida there is a pair of eyes on the "head" or the cephalothorax respectively. The eyes in the Arachnida are all (Fig. 510) of the type of the *ocelli* of Insects, except the central eyes of the Scorpions (Fig. 511) and the compound eyes of Limulus. The former are intermediate in character between ocelli and faceted eyes, possessing the single cuticular lens (*lens*) of the ocellus, and resembling the faceted eye in having the retinal cells arranged in groups corresponding to ommatidia. Each retinula, composed of five cells, contains a thick axial rod or rhabdome (*rhabd.*).

In Limulus the compound eye has a continuous chitinous cornea-lens of the nature of a thickening of the cuticle. This, though non-faceted, differs

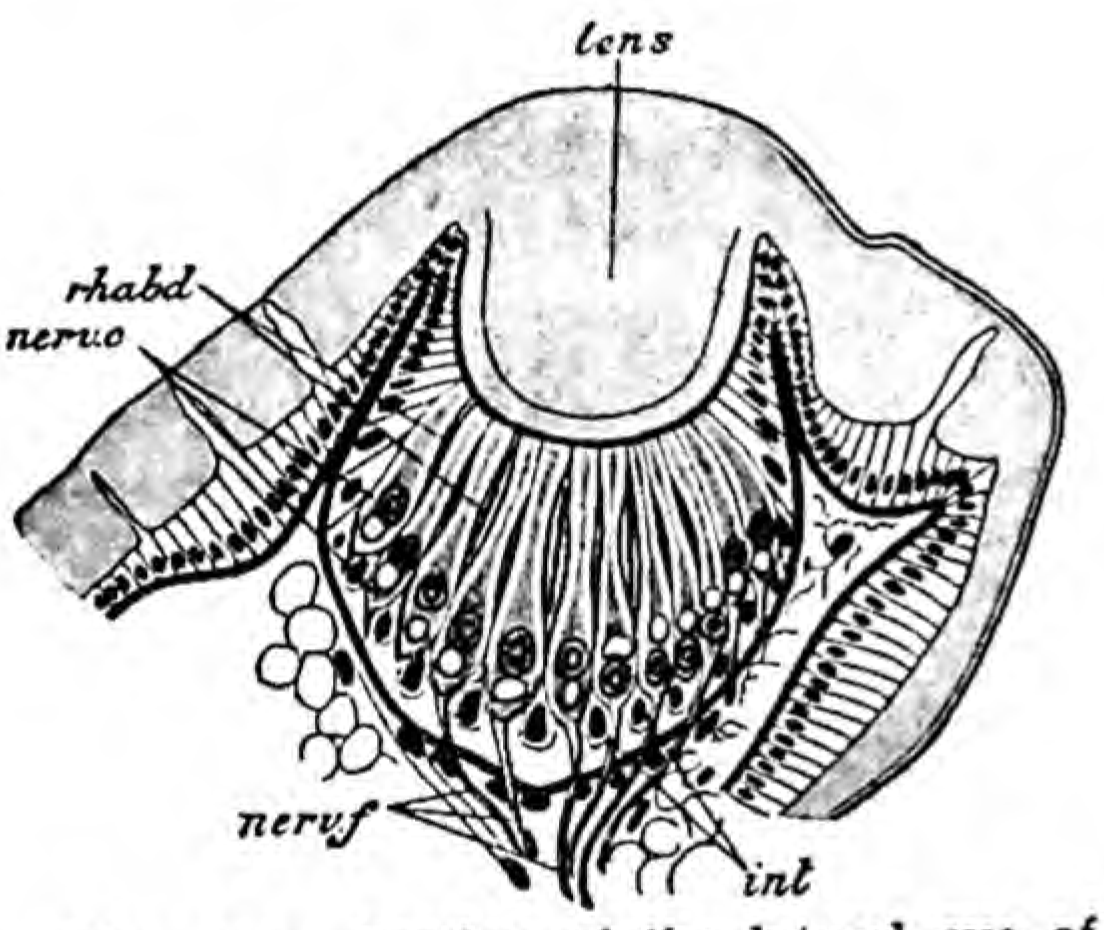


FIG. 510.—Section of the lateral eye of **Euscorpius italicus.** *int.* intermediate cells; *lens*, cuticular lens; *nerv. c.* terminal nerve-cells; *nerv. f.* nerve-fibres of optic nerve; *rhabd.* rhabdomes. (After Lankester and Bourne.)

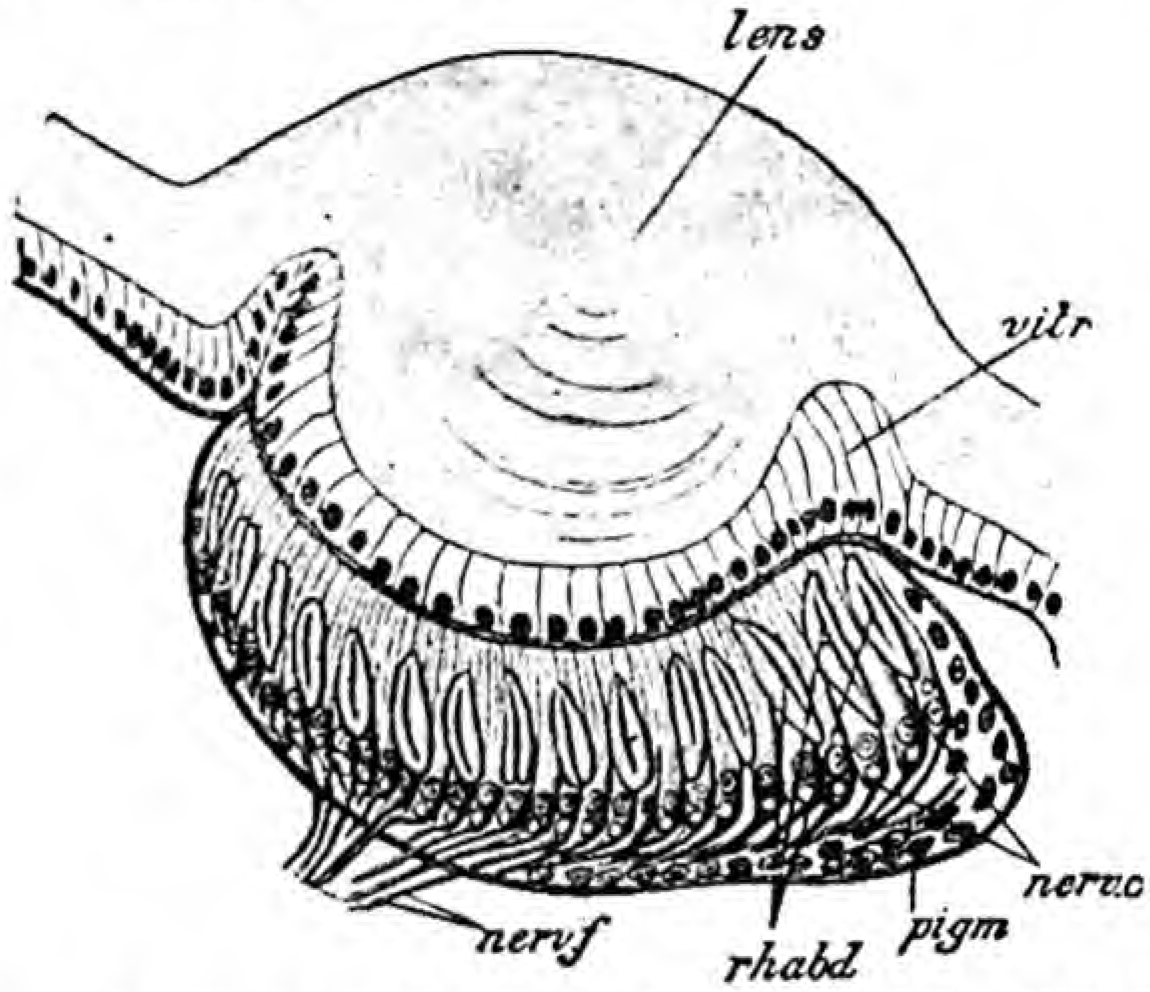


FIG. 511.—Section of the central eye of **Euscorpius.** Letters as in preceding figure. *pigm.* cells containing pigment; *vtr.* vitreous body (a specialized part of the ectoderm). (After Lankester and Bourne.)

from the corresponding part in the compound eye of the Scorpion in being produced internally into a number of conical papillæ, each of which lies over one of the ommatidia and may be looked upon as its lens.

A considerable variety is observable in the exact arrangement of the parts of the **reproductive apparatus** in different groups of the Arachnida. In general, *testes* or *ovaries* are either paired or (more rarely) unpaired tubes, with paired *vasa deferentia* or *oviducts*, which unite in a median duct opening on the exterior by an unpaired genital opening. Viviparity is exceptional. In the Spiders the ovaries (Fig. 506, *ov.*) are two wide tubes, on the surface of which follicles project prominently; sometimes they unite into a single circular ovary. There are two short oviducts even when the ovary is single; these unite in a median *vagina*, which opens on the exterior by a median genital aperture at the base of the abdomen. One, two, or three *receptacula seminis* (*rec. sem.*)

are present, and either open into the vagina or independently on the surface. In the male there are two elongated tubular *testes* with two narrow and often greatly coiled *efferent ducts*, which unite in a short median *vas deferens*, the aperture of which is on the base of the abdomen between the first pair of stigmata. The pedipalpi of the male (Fig. 512) are modified to act as intromittent organs: the terminal segment is swollen, and contains a twisted tube (*sph.*) into which the sperms from the reproductive aperture are received in order to be transferred in the act of copulation to the reproductive aperture of the female. The eggs of spiders are laid in nests or cocoons, and are usually guarded by the mother, sometimes carried about by her.

In their **mode of life** the Arachnida present almost as great a diversity as the Insecta. Some Acarina are parasites throughout life. Most of the other groups of Arachnida are predaceous—preying for the most part on Insects or other Arachnids. To capture the Insects which constitute their food, the majority of Spiders construct a web formed of the threads secreted by the arachnidium (Fig. 506, *arach.*). The primary function of the threads formed from the secretion of the spinning organ is to constitute the material for the manufacture of a cocoon enclosing the eggs, and in some Araneids this is the sole purpose to which they are devoted. In others there is added a nest for the protection of the eggs and of the parent itself; this in many cases becomes a permanent lurking-place which the Spider inhabits at all seasons, and from which it darts out to capture its prey; the nest of the Trap-door Spider has a closely fitting hinged lid. In very many Spiders the secretion is used mainly to form the web by means of which the prey is snared, and frequently also a nest in which the Spider lies in wait. A subsidiary function of the threads is to aid in locomotion, the Spider being enabled by means of them to let itself down safely from considerable heights, and even to float in the air.

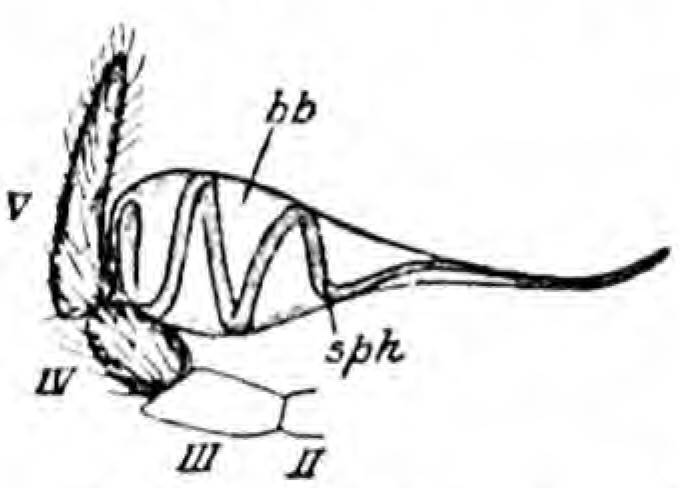


FIG. 512.—Pedipalp of male of **Aranea diademata.** *II. III. IV. V.* podomeres: *bb*, sac; *sph.* spiral tube. (After Leuckart.)

Some of the Mites are parasitic; others feed on various kinds of fresh or decaying animal or vegetable substances. Most free Acarina are terrestrial; some are aquatic. The blood-sucking Ticks *Boophilus annulatus* and *Ornithodorus moubata* are the carriers of Spirochæte-born diseases, viz. the *Texas fever* of Cattle and the *relapsing fever* of Man respectively.

The Xiphosura are marine, living at a depth of a few fathoms in warm seas, burrowing in sand; their food consists of various kinds of marine Annelids.

Geological History.—The most ancient of the living groups of the Arachnida are the Xiphosura and the Scorpions, the latter being represented in Silurian rocks by various fossil forms not differing very widely from those existing at the present day. A member of the Acarina has been found in the Devonian

Rhynie Chert. The earliest known fossil Spiders have been found in deposits of Carboniferous age; and remains of Pedipalpida occur in the same formation. In Tertiary deposits there have been found representatives of all the principal groups of living Arachnida.

The earliest fossil-remains of Xiphosura that have been found occur in strata of the Silurian period. Other fossil species occur in later formations. These are all nearly related to the living species of Limulus. The Eurypterida, as already noted, are entirely Palæozoic, ranging from the Ordovician rocks to the Devonian.

APPENDIX TO THE ARACHNIDA

THE PYCNOGONIDA AND THE LINGUATULIDA.

These groups, though not in any way related to one another, and of doubtful relationships to the Arachnida, are, as a matter of convenience, mentioned together here.

THE PYCNOGONIDA (PANTOPODA).

These are marine Spider-like Arthropods (Fig. 513) in which the body consists of a cephalothorax composed of an anterior proboscis (*s.*), three head-segments, and one

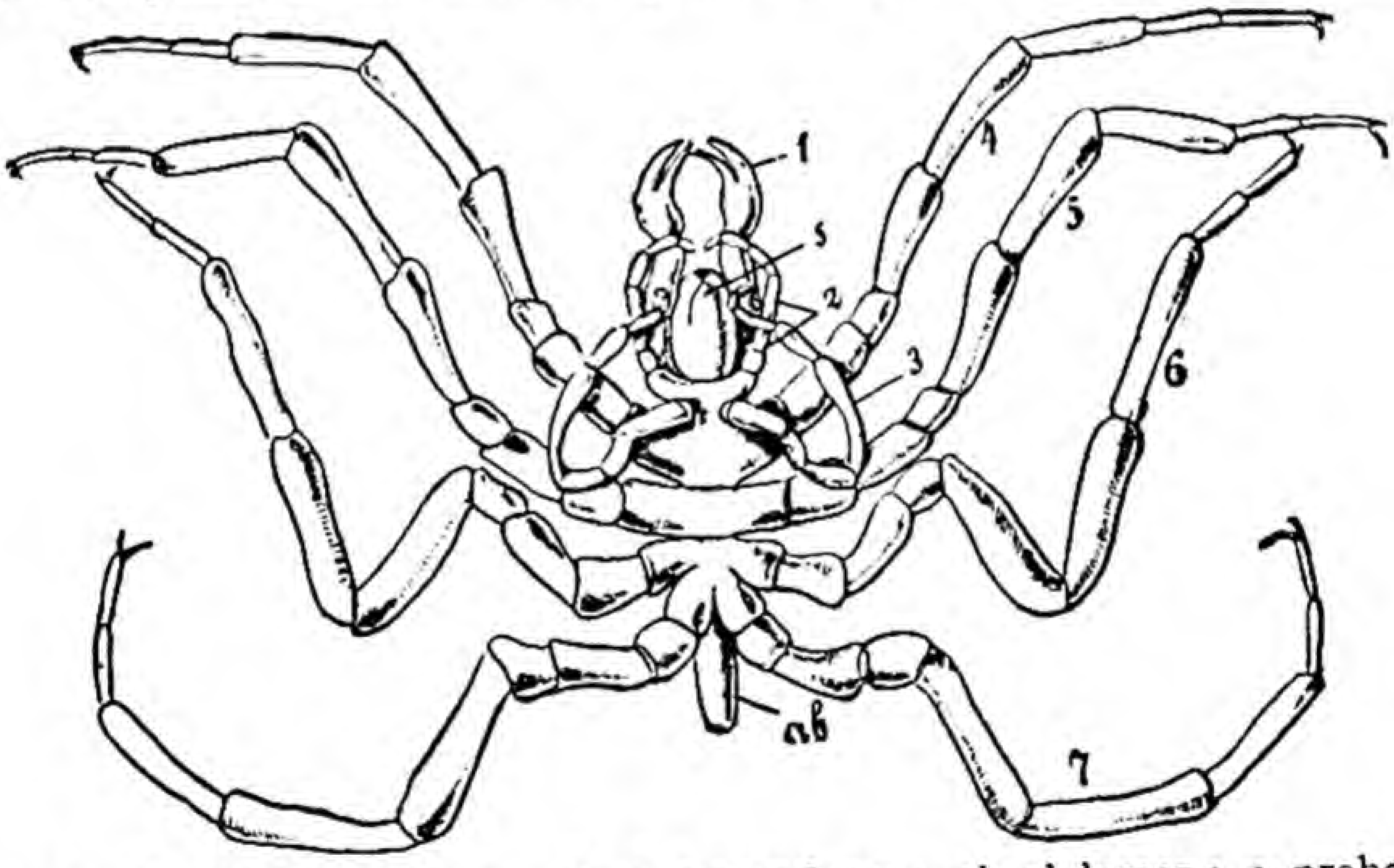


FIG. 513.—**Nymphon hispidum.** *1—7*, appendages; *ab.* abdomen; *s.* proboscis. (From Lang, after Hoek.)

thoracic segment, followed by three free thoracic segments and a rudimentary abdomen (*ab.*). The cephalothorax bears usually four simple eyes and four pairs of appendages, the first of which may be chelate. To these succeed a pair of ovigerous legs (3), and the first pair of thoracic legs (4). The free thoracic segments bear lateral processes for the articulation of the remaining three pairs of legs. A number of Antarctic species have five and more pairs of legs. The rudimentary abdomen (*ab.*) is devoid of appendages.

Diverticula from the mesenteron penetrate for a considerable distance into the limbs. Malpighian vessels are absent. There is a tubular heart with two or three pairs of ostia. Organs of respiration are absent. The nervous system consists of brain, sub-œsophageal ganglia and three other ganglia in the cephalothorax, and one or two small pairs in the abdomen. The testes in the male are partly, and the ovaries in the female either partly or completely, contained in the bases of the thoracic appendages on which they open. In the male 4—7 cement-glands are situated in the fourth joints of certain of the appendages;

their secretion cements the eggs together into masses which are carried on the ovigerous legs of the male, and in one species on those of the female also.

A metamorphosis occurs in most cases. The larva usually has three pairs of appendages, so that it bears a superficial resemblance to a nauplius; but the appendages are simple, and in other respects the larva has no essential likeness to the nauplius form. Additional segments with their appendages are formed behind the original three until the form of the adult is completed. Different kinds of Pycnogonids occur at various depths from between tidal limits to considerable depths in the ocean. The larvæ of the species of one genus are internal parasites in certain hydroid Zoophytes.

The Linguatulida (Pentastomida).

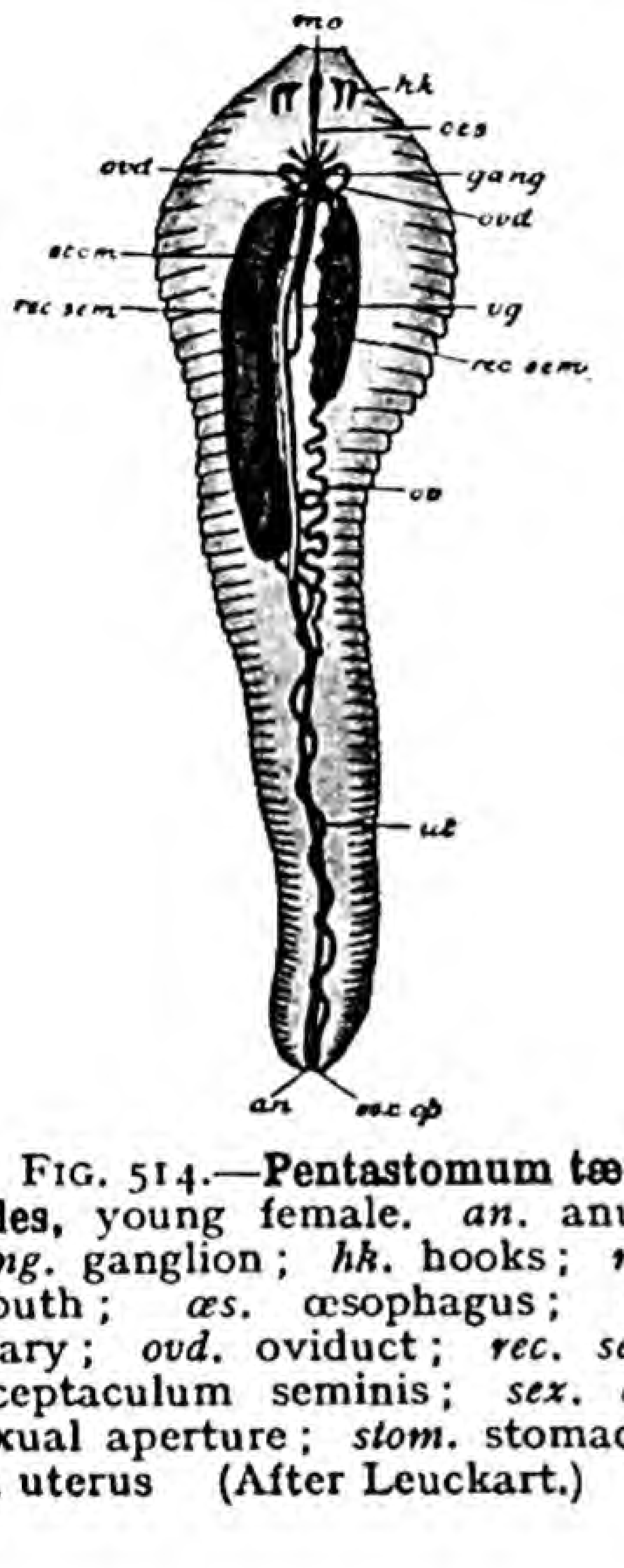


Fig. 514.—**Pentastomum tænioides**, young female. *an.* anus; *gang.* ganglion; *hk.* hooks; *mo.* mouth; *œs.* œsophagus; *ov.* ovary; *ovd.* oviduct; *rec. sem.* receptaculum seminis; *sex. ap.* sexual aperture; *stom.* stomach; *ut.* uterus (After Leuckart.)

The Linguatulida (Fig. 514) are parasitic animals, which, when superficially examined, present little appearance of affinity with the Arthropoda. The body is completely worm-like, not divided into regions, and presenting only a superficial annulation, which in no way corresponds with division of the body into segments. The sole representatives of limbs are four hooks (*hk.*) at the sides of the mouth. The muscular fibres are striated. The alimentary canal is simple and straight. Heart and organs of respiration are wanting. The nervous system is greatly reduced. A narrow nerve-collar surrounds the œsophagus, presenting no brain-enlargement, and connected behind with a single ventral nerve-mass. Sense-organs are absent.

Some species of Pentastomum are in the adult condition parasites in the lungs of snakes. One species (*Pentastomum tænioides*) inhabits certain cavities—the frontal sinuses and maxillary antra connected with the nasal chambers—in the Dog and Wolf. Its embryos, escaping and falling on grass and other herbage, which form the food of Hares and Rabbits, are taken up by these animals, and perforating the wall of the alimentary canal, by means of a boring apparatus composed of several chitinous pieces, lodge themselves in the liver, where they become encysted and undergo a metamorphosis. Afterwards they leave the cysts and move about. If the young Pentastomum should be received into the mouth of a Dog (still contained probably in most cases in the tissues of the Hare or Rabbit) it may find its way to the frontal sinuses or maxillary antra, there to undergo its final transformation into the adult form. The larva possesses two pairs of short legs.

APPENDIX TO THE ARTHROPODA.

THE ONYCHOPHORA.

The class Onychophora comprises only the aberrant Arthropod *Peripatus*, with several sub-genera (or closely allied genera), which differs very widely in certain important features of its organization from all the rest of the Arthropoda, and in some respects enables us to bridge over the interval between the latter and some of the lower phyla, more particularly the Annelida.

General external features.—Peripatus (Fig. 515) is a caterpillar-like animal of approximately cylindrical form, and not divided into segments; it has a fairly well-marked head, and a series (14–42, according to the species) of pairs of short stumpy appendages. The integument is thrown into a number of fine transverse wrinkles, and is beset with numerous conical papillæ, each

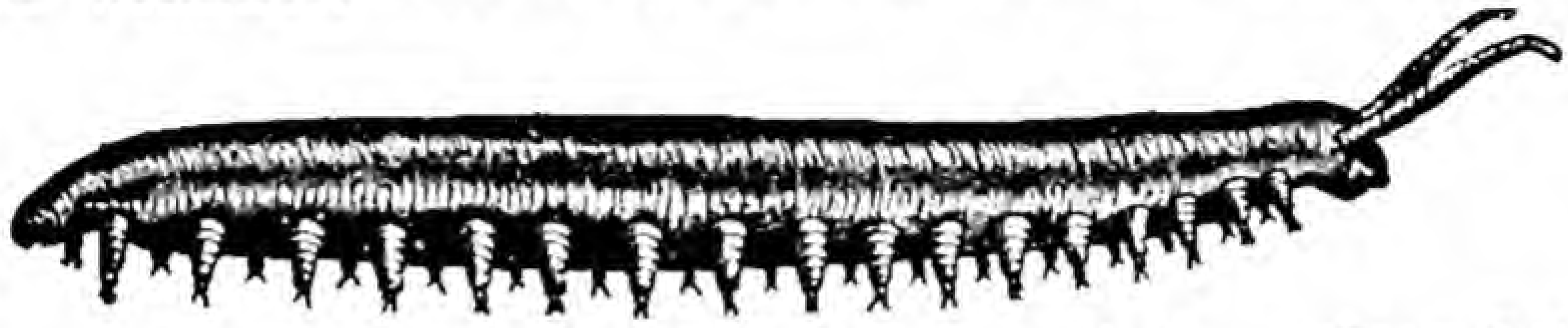


FIG. 515.—**Peripatus (Peripatopsis) capensis,** lateral view. (From Balfour.)

capped with a little chitinous spine. The head (Fig. 516) bears a pair of antennæ, a pair of eyes, a pair of jaws, and a pair of short processes known as the *oral papillæ.* The antennæ are made up of a number of short rings bearing minute spines. The eyes are constructed somewhat after the model of the chætopod eye as described on p. 316. On the surface of the oral papillæ

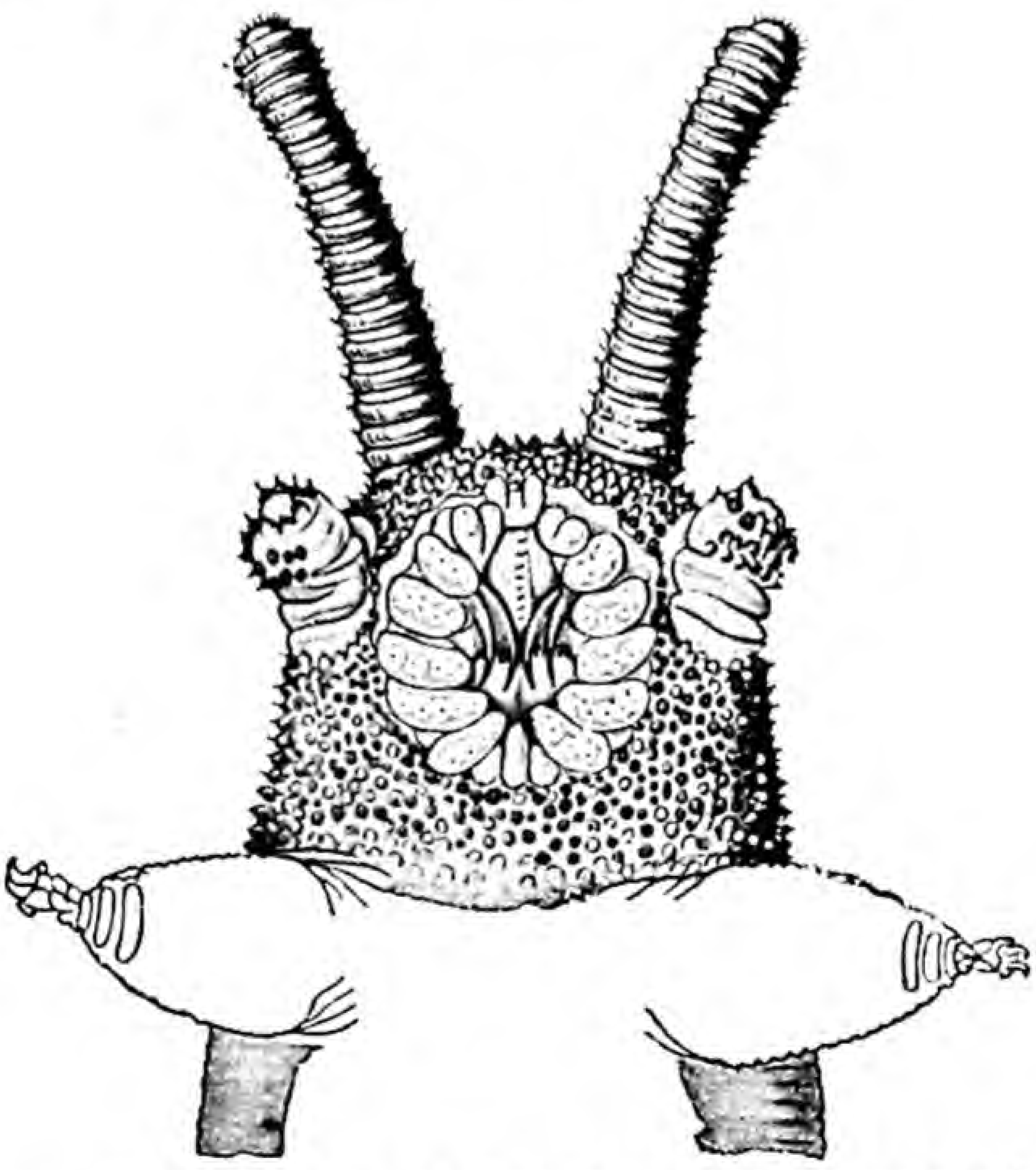


FIG. 516.—Ventral view of head of **Peripatus (Peripatopsis) capensis,** with antennæ, jaws, oral papillæ, and first pair of legs. (After Balfour.)

are situated the apertures of a pair of glands—the *slime-glands.* Each *jaw* is composed of two curved, falciform, pointed, chitinous plates, the inner toothed on its posterior concave edge; they lie at the sides of the mouth enclosed by a circular lip. The jaws, as well as the oral papillæ, are developed as modified limbs.

The *legs* are not jointed, but rows of papillæ give them a ringed appearance; each consists of a conical proximal part and a small distal part or *foot*, the latter terminating in a pair of horny claws.

The ventral surface is reddish in colour, the dorsal darker: the latter presents an elaborate pattern—which varies greatly in different individuals—produced by minute mottlings of various colours and tints, green, red, and brown, and the arrangement of these in stripes and bands.

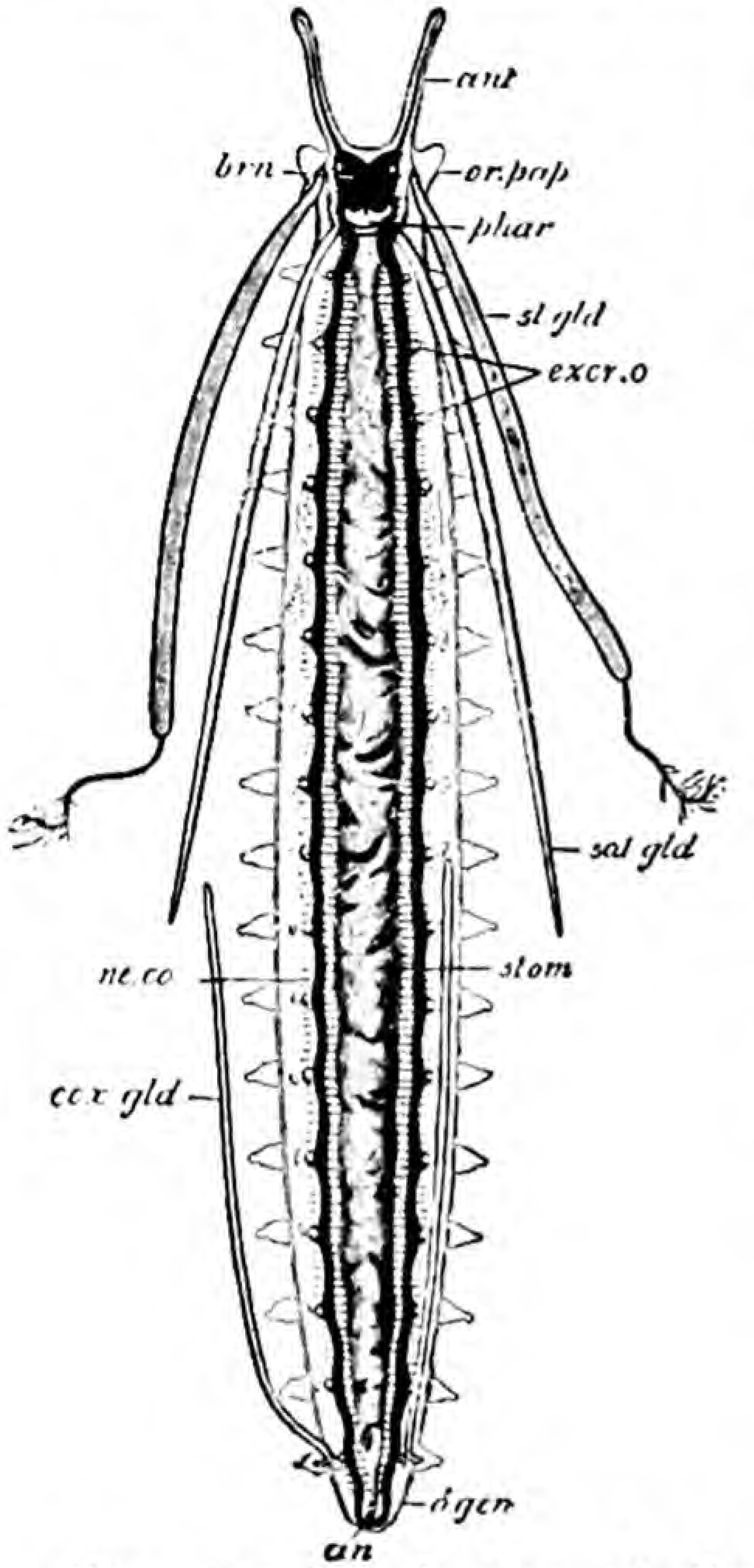


FIG. 517.—Dorsal view of the internal organs of **Peripatus**. *an.* anus; *ant.* antennæ; *brn.* brain; *cox. gld.* coxal gland of the seventeenth leg; *excr. o.* excretory organ; *♂ gen.* male genital aperture; *ne. co.* nerve-cord; *or. pap.* oral papillæ; *phar.* pharynx; *sal. gld.* salivary gland; *sl. gld.* slime-gland; *stom.* stomach. (Combined from Balfour.)

Body-wall and **body-cavity.**—The wall of the body consists of a cuticle, a layer of deric epithelium with an underlying layer of fine fibres, a layer of circular muscular fibres, and one of longitudinal muscular fibres divided into a series of bundles. A layer of epithelium lines the wall of the body-cavity and invests the contained organs. Incomplete muscular partitions divide the cavity into a median and two lateral compartments, in addition to the pericardium, the space in which the heart is lodged; the lateral compartments send prolongations into the legs. The body-cavity is not a cœlome, but, as shown by its development, a hæmocœle—an extension of the blood-vascular system—as in the Crustacea.

The **enteric canal** (Fig. 517) begins with a small *buccal cavity*, formed secondarily by the union of a ring of papillæ and folds surrounding the true mouth into a circular lip: it encloses the bases of the jaws and bears on its roof a slight prominence, the *tongue*, with a row of small spines or teeth. This is followed by a thick-walled *pharynx* (*phar.*) leading to a narrow *œsophagus*. The part which follows, the *mesenteron* or stomach-intestine, a wide somewhat thin-walled tube, extends nearly to the posterior end of the body. The narrower *rectum* leads to an anal aperture situated on the last segment of the body. A diverticulum leading backwards from the buccal cavity, where it passes into the pharynx, receives the secretion of two long, narrow, tubular *salivary glands* (*sal. gld.*).

Circulatory system.—The *heart* is an elongated tube running through nearly the entire length of the body. It presents a number of pairs of valvular ostia arranged segmentally—*i.e.*, one opposite each pair of legs. It is enclosed in a pericardial sinus imperfectly cut off from the general body-cavity by a longitudinal partition.

The **organs of respiration** (Fig. 518) are delicate, unbranched or rarely branched, *tracheal tubes*, lined with a thin chitinous layer exhibiting fine transverse striations. Groups of these open in little depressions of the integument, the tracheal pits (*tr. p.*), the external openings of which are known as the *stigmata* (*tr. o.*). The stigmata are usually distributed irregularly over the surface, with a tendency to arrangement in rows in *P. capensis*. By means of these tubes air is conveyed to all parts of the body.

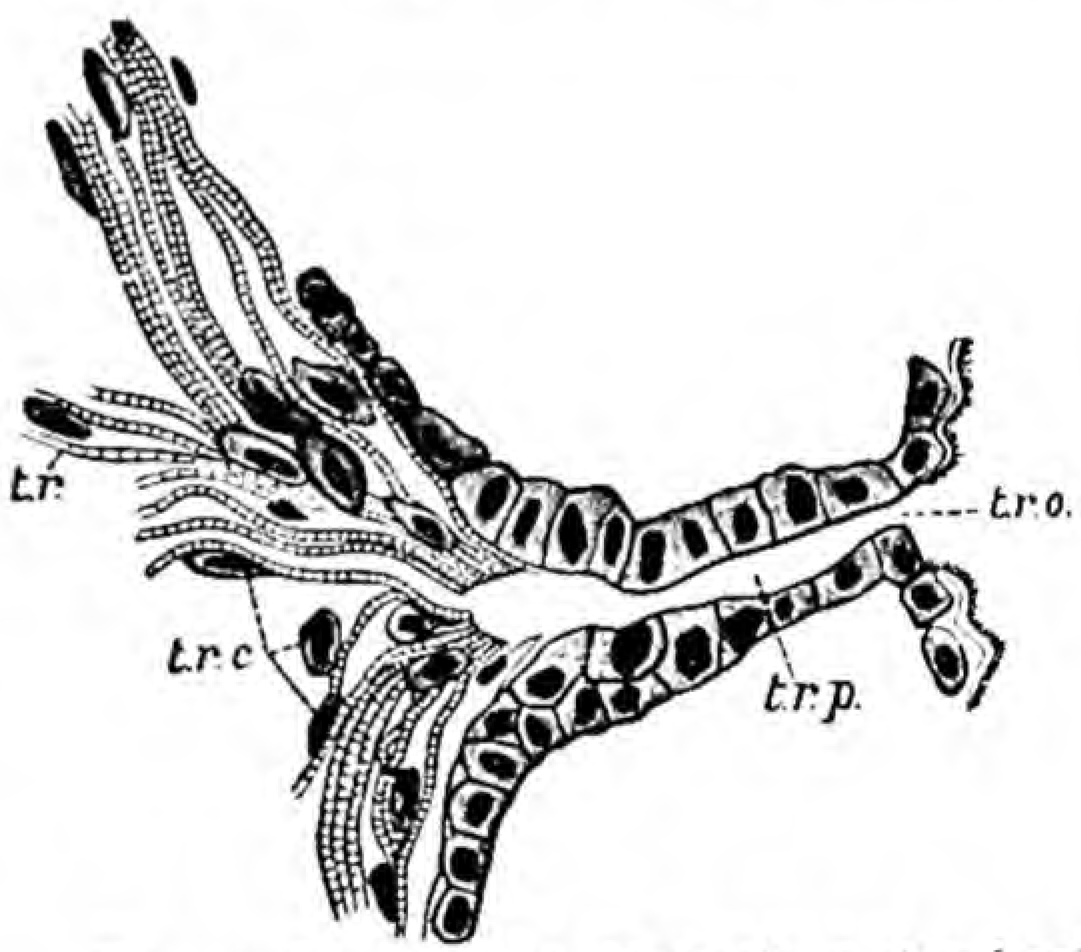


FIG. 518.—Section through a tracheal pit and diverging bundles of tracheal tubes of **Peripatus.** *tr.* tracheæ; *tr. c.* cells in walls of tracheæ; *tr. o.* tracheal stigma; *tr. p.* tracheal pit. (From *Camb. Nat. Hist.*, after Balfour.)

A series of pairs of glands, the **coxal** or **crural glands** (Fig. 517, *cox. gld.*), lie in the lateral compartments of the body-cavity, and their ducts open on the lower surfaces of the legs just outside the apertures of the excretory ducts. They are absent in the female except in *P. capensis*, and their number and arrangement differ in the males of the various species. Also opening on the ventral surfaces of the legs is a series of thin-walled vesicles—the **coxal organs**: these occur in both sexes and are capable of eversion and retraction. A pair of large glands—the **slime-glands** (*sl. gld.*)—opening at the extremities of the oral papillæ, may be modified coxal glands: the secretion of these is discharged in the form of a number of fine viscid threads when the animal is irritated, and appears to serve a defensive purpose.

The **nervous system** consists of a *brain* (*brn.*) situated in the head, and of two *longitudinal nerve cords* (*ne. co.*) which run parallel with one another throughout the body to the posterior end, where they join together behind the anal aperture. A number of very fine transverse commissures, more numerous than the segments (*i.e.*, than the pairs of limbs), connect the two cords together to form a ladder-like nervous system comparable to that of some of the Flat Worms. The cords are very slightly swollen opposite each pair of limbs: nerve-cells cover them uniformly throughout their entire length. The brain gives off nerves to the antennæ. The nerves to the jaws are given off just where the brain passes into the longitudinal nerve cords.

The excretory organs (Fig. 519) are situated in pairs in the lateral compartments of the body-cavity, and open on the lower surfaces of the legs at their bases. Each excretory organ consists of a thin-walled closed internal vesicle, representing a section of the cœlome, into which by a funnel-shaped aperture leads a looped tube (*s. c.*), and a dilated *terminal vesicle* (*s.*), situated close to the external opening. The excretory organs can be described as modified cœlomoducts. The salivary glands are, as shown by the study of their development, specially modified excretory organs, as apparently also are a pair of glands—the *anal glands*—opening close to the anus.

Reproductive organs.—Peripatus has the sexes distinct. In the female there are two tubular *ovaries*, a pair of *oviducts*, and two *uteri*, the latter in the form of long curved tubes which unite behind in a median vagina opening on the exterior on the ventral surface, between the legs of the last pair or behind them. In the oviparous forms the opening is situated at the end of a long cylindrical process—the *ovipositor*. In some species, connected with each uterus where it leaves the ovary, are two diverticula—the *receptaculum seminis* and *receptaculum ovorum*. In certain species one or other of these may be absent.

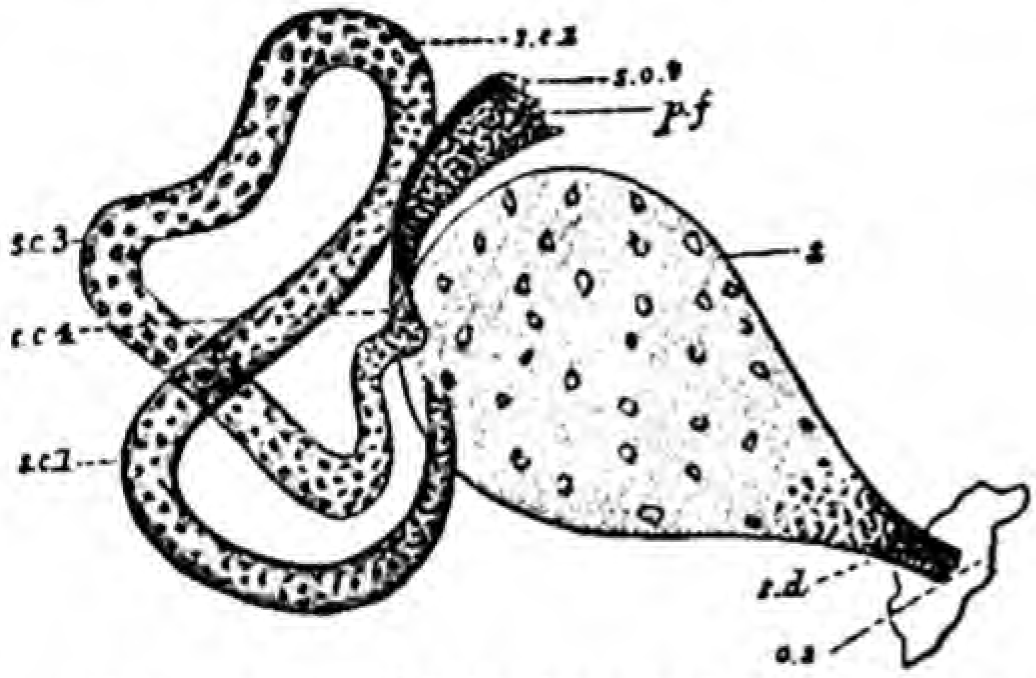


FIG. 519.—**Peripatus capensis**, excretory organ from the ninth pair of legs. *o. s.*, external opening; *p. f*, internal opening into the lateral compartment of the body-cavity; *s*, vesicle; *s. c.* 1, *s. c.* 2, *s. c.* 3, *s. c.* 4, successive regions of coiled portion; *s. o. t.*, third portion broken off at *p. f.* from the internal vesicle, which is not shown. (From the *Camb. Nat. Hist.*, after Balfour.)

In the male there are two tubular *testes*, each with a narrow *vas efferens* opening by a funnel-like aperture into a *vesicula seminalis*; this is followed by a long, narrow, coiled *vas deferens*. The two vasa deferentia unite together to form a median tube—the *ductus ejaculatorius*—opening on the exterior, in the same position as the vagina of the female. The wall of the proximal part of the ejaculatory duct is glandular, and secretes a substance forming complicated cases which enclose masses of sperms to form spermatophores.

Development.—The differences between the species of Peripatus as regards the cleavage of the egg and the formation of the germinal layers as described by various observers are very considerable. Nearly all the species are viviparous, but in some the egg, before the completion of embryonic development, is enclosed in a well-formed shell, and in certain species the eggs pass out to the exterior before the emergence of the embryo. In some species the egg encloses a considerable amount of food-yolk, in others the quantity of food-yolk is small, and nutriment is obtained from the parent.

In *P. novæ-zealandiæ* there is a superficial cleavage. The zygote-

nucleus is itself superficial, and cleavage results in the development of a number of nuclei, each with its island of protoplasm, which arrange themselves on what is destined to become the dorsal side (Fig. 520, *A*), opposite the site of the future blastopore, while some pass inwards to the central part of the ovum. The peripheral nuclei multiply rapidly and grow round the yolk so as completely to enclose it except on a small space (blastopore) in the middle of the ventral side (*B*). There a thickening takes place, and an involution of the lips of the blastopore results in a sort of invagination, the floor of the invagination-cavity being formed of yolk with scattered nuclei.

In another species—*Peripatopsis capensis*—the cleavage is total. A peripheral ectodermal layer becomes formed, enclosing a central mass of

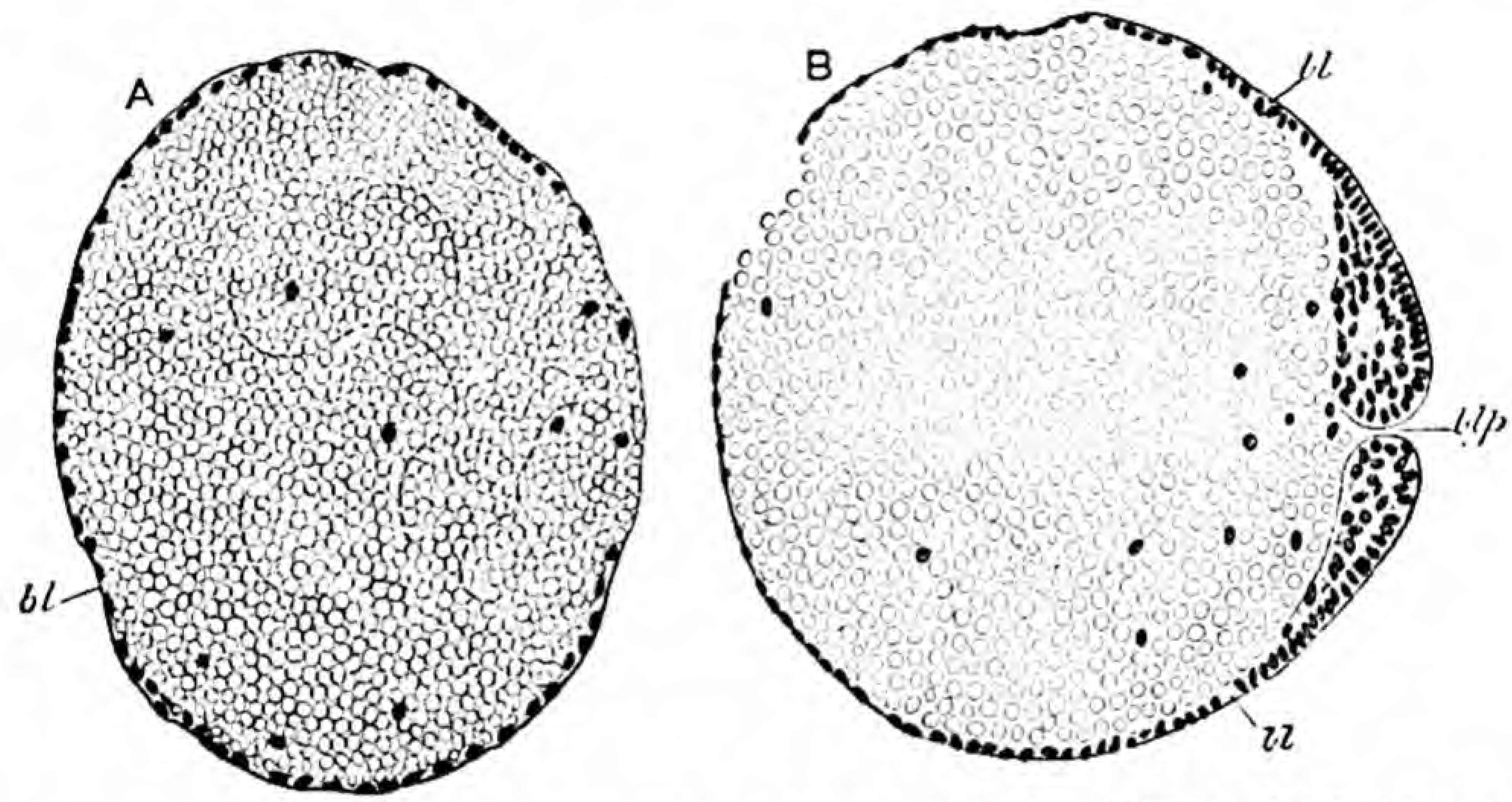


FIG. 520.—Two early stages in the development of **Peripatus (Peripatoides) novæ-zealandiæ.** *A*, transverse section of an ovum in which the yolk is nearly covered by the blastoderm (*bl.*); *B*, transverse section of an ovum in which the blastopore (*blp.*) is formed. (After Sheldon.)

cells—the endoderm—except at one point where a small area, the blastopore, is uncovered.

In accordance with the smaller size of the ova and the relationship of the embryo with the wall of the uterus, the South American species show a totally different mode of development. The eggs, which are almost entirely devoid of yolk, undergo a total and tolerably equal process of cleavage. Even at this stage the embryo, which increases considerably in size, appears to receive nutrient lymph from the uterine wall. Later an intimate connection is established between the embryo and a modified area of the uterine epithelium, the *placenta* thus formed evidently providing, like the placenta of Mammals, for the nourishment of the embryo.

In *P. capensis* (Fig. 521) proliferation of cells gives rise to an oval thickening behind the elongated blastopore. The mesoderm takes its origin at this point and extends forwards in the form of two *germinal bands*, one on the

right of the blastopore and the other on the left. These bands undergo a division into rudiments of segments—the division beginning in front. The lips of the blastopore meanwhile become approximated, and fuse throughout the greater part of their length, leaving only an anterior and a posterior opening; these go to form the mouth and the anus respectively. The division

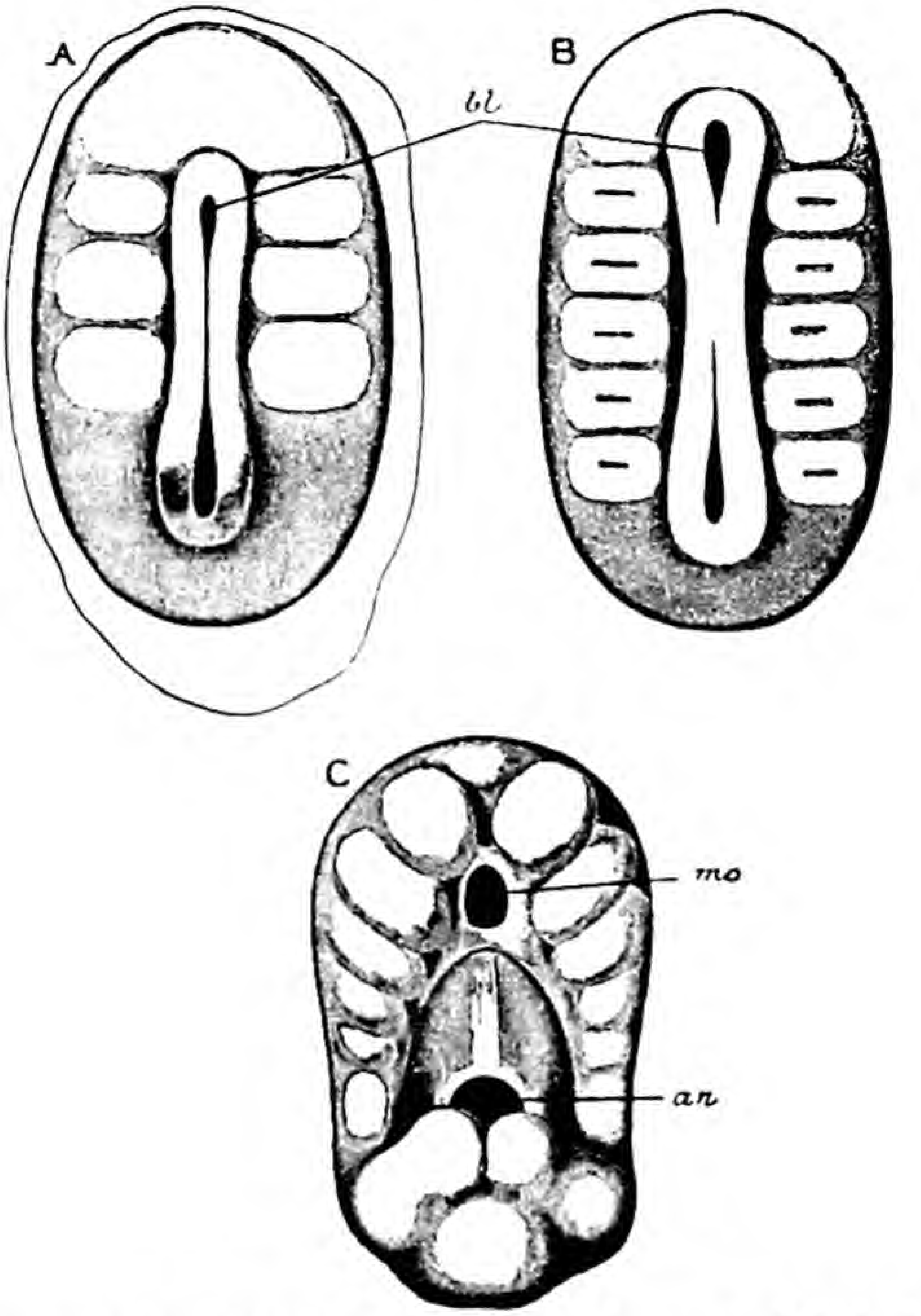


FIG. 521.—Three somewhat later stages in the development of **Peripatus capensis,** showing the mode of closure of the blastopore and the appearance of the primitive segments. *A*, stage in which the blastopore (*bl.*) has the form of an elongated slit; *B*, stage in which the blastopore is closing up in its middle part; *C*, stage in which the blastopore has become closed up except the anterior part which has gone to form the mouth (*mo.*), and the posterior part which has formed the anus (*an.*); the whole embryo has now become strongly curved towards the dorsal side. (After Balfour.)

into segments soon becomes well marked. The cavities in the mesoderm of the segment give rise only to the internal vesicles of the excretory organs and the generative ducts, which thus alone represent the cœlome. The greater part of the excretory tubule and the terminal vesicle are probably of ectodermal origin. At the anterior end the head lobes become distinguishable.

The body elongates, and the head and trunk become differentiated. The limbs now arise as ventro-lateral outgrowths which are developed from before backwards. The jaws originate in the same manner as the limbs, as external projections, and only later become enclosed by folds that give rise to the buccal cavity of the adult.

Distribution.—The various species of Peripatus are all terrestrial, and are found in damp localities, under bark, or dead timber, or stones. Some twenty-nine species occur in the Neotropical region; one in South America; eight in Africa; four in Malaya; one in New Britain, and eight in Australasia.

Relationships.—Peripatus presents striking points of resemblance to both the Arthropoda and the Chætopoda. The development is in the main arthropodan, especially as regards the mode of cleavage (at least in the forms with much food-yolk, which are probably the more primitive), the mode of closure of the blastopore, and of the development of the germinal bands. Arthropodan also are the relatively large size of the brain and the presence of tracheæ, the character of the heart with its pairs of ostia, together with the clawed appendages, and the jaws in the form of modified limbs. The excretory organs, on the other hand, and their modification in certain segments to form the gonoducts, which are ciliated internally, are annelidan in character; and the slime-glands and coxal glands have been said to correspond to the setigerous sacs of the Chætopoda. The nervous system is peculiar, and is most nearly paralleled among the Platyhelminthes and the Mollusca. Also peculiar, and serving to distinguish Peripatus from the rest of the Arthropoda, are the large number of stigmata and their irregular arrangement, the presence of only a single pair of jaws, and the nature of the cuticle.

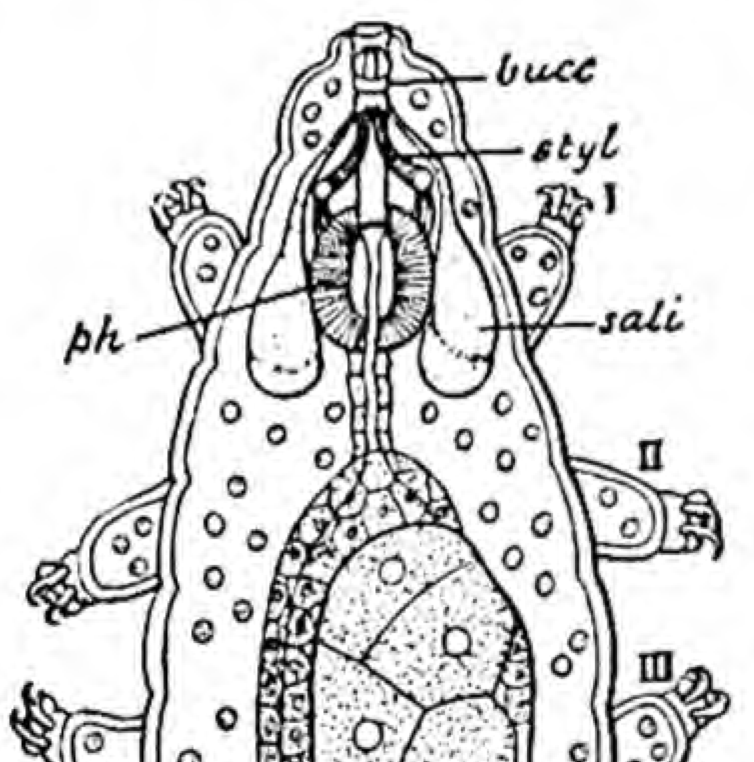


FIG. 522.—**Macrobiotus hufelandi.** I—IV, appendages; *bucc.* buccal cavity; *gld.* accessory gland; *mal.* Malpighian tube; *ov.* ovary; *rect.* rectum; *sali.* salivary glands; *stom.* stomach; *styl.* teeth. (From Hertwig's *Lehrbuch*, after Greef and Plate.)

THE TARDIGRADA.

The Tardigrada ("Bear-animalcules") are soft-skinned animals (Fig. 522) of minute size, not exceeding a millimetre in length. The body is unsegmented and not distinguishable into regions, except that in some a slight constriction separates off an anterior part or head from the rest. The mouth is provided with a sucking proboscis. There are four pairs of short unjointed legs (I—IV), the last of which is terminal, and each is provided with two or four claws. The mouth is surrounded by papillæ; the buccal cavity contains a pair of horny, sometimes partly calcified, teeth (*styl.*). The ducts of a pair of salivary (?) glands (*sali*) open into the cavity of the mouth; there is a muscular pharynx (*ph.*), a narrow œsophagus, and a wide mesenteron (*stom.*); the anus is sub-terminal, situated

in front of the last pair of limbs. A pair of tubes (*mal.*) which open into the terminal part of the intestine are perhaps representatives of Malpighian tubes. The muscles are all non-striated. There are no organs of respiration, and heart and blood-vessels are likewise absent. There are a brain and a ventral nerve-cord with four ganglia. Two eye-spots situated at the anterior end are the only representatives of sense-organs. The gonads in both sexes are saccular, and open into the terminal part of the intestine. Cleavage is complete and regular. The young animal at one stage has only two pairs of rudimentary legs, but develops the full number before being hatched. The larva possesses a head and four distinct segments.

Some of the Tardigrada live among damp moss; others in fresh or in salt water.

Relationships of the Air-breathing Arthropoda.[1]

Notwithstanding the existence of some striking superficial resemblances between the Arachnida and the Insecta, the evidence afforded by anatomy and embryology points to the conclusion that there is no direct genetic relationship between the two groups. The occurrence in both of a peculiar form of respiratory organs, the tracheæ, seems at first sight to indicate such a relationship; but the evidence of an independent origin is so strong that it must be supposed that the tracheæ have been independently developed in the two classes. The most important points of difference are—the separation of head and thorax in the Insecta, the mode of development of the eyes, the presence in the Arachnida of an extensive "liver," and (perhaps) the endodermal origin of the Malpighian tubes in the latter class.

Resemblances between Limulus and the Scorpions are readily apparent. In both there is a cephalothorax bearing six pairs of appendages, together with two median and several lateral eyes. The appendages in both are all originally post-oral, the first pair becoming pre-oral in course of growth, and the ganglia belonging to it coalescing with the brain. The upper lip between the bases of these appendages is similarly developed in both. The pair of processes situated behind the sixth pair of appendages, which in Limulus form the chilaria, are represented in the Scorpions by a small pentagonal plate in front of the operculum. The abdomen of Limulus corresponds to the pre- and post-abdomen of the Scorpion; it contains only seven segments, and the telson. A certain amount of correspondence is also traceable in the appendages of the abdomen. In both the first pair form the operculum; in the Scorpion the second pair form the pectines, while the rest disappear; in Limulus all persist as the lamelliform appendages to which the book-gills are attached. In structure there is considerable similarity between the book-gills of Limulus and the book-lungs of the Scorpion, but how far they are equivalent to one another remains doubtful in view of the difference in their position, the book-gills being attached to the dorsal surface of the abdominal appendages and the book-lungs sunk within the segments.

[1] The *Xiphosura*, and also the *Pentastomida*, though not air-breathing, are discussed here.

The presence in both of the large "liver," the presence of a circum-œsophageal artery, of a cartilaginous endosternite, and of a pair of coxal glands on the basal joints of the fifth pair of appendages, are some of the points of correspondence in the internal anatomy.

It seems probable that the air-breathing Arachnida were derived through Limulus-like ancestors from primitive Crustacea, and that the tracheæ were developed without genetic relationship with those of the other air-breathing groups—perhaps as modifications of the pulmonary sacs, the latter having been originally derived from gills like those of Limulus. That air-tubes can be developed in air-breathing members of what are, fundamentally, aquatic groups is shown by the case of certain terrestrial Isopoda among the Crustacea (p. 449).

There are evident points of resemblance between the Chilopoda among the "Myriapoda," and the Insecta. The Insects are more highly specialized, and have their structure modified in adaptation to a special mode of locomotion. One of the most striking points of difference is the indefiniteness in the number of the segments in the "Myriapoda," and their constant and definite arrangement in the Insecta. The well-defined thorax of the Insects is wanting in the "Myriapods." The presence in both groups of a sharply marked-off head bearing antennæ and jaws is an important point of resemblance; so is the absence in both of the voluminous "liver" of the Crustacea and Arachnida.

Perhaps the most satisfactory way of describing the affinities of the various groups of Arthropods may be to assume that an intermediate link between the Annelida and the existing Arthropoda may have been constituted by hypothetical, primitive forms from which the Onychophora, the Crustacea, the Insecta, and the Myriapoda are supposed to have been evolved in the one direction, and the Crustacea, Eurypterida, Xiphosura, and air-breathing Arachnida in the other.

On account mainly of general resemblances to the Spiders, the Pycnogonida have frequently been grouped with the Arachnida, and attempts have been made to homologize their appendages with those of the Spiders and Scorpions. A close relationship with the Arachnida, however, cannot be traced. The position of the Linguatulida is a matter of uncertainty. In the absence of organs of respiration and excretion, the only feature in the adult which distinctly points to arthropod affinities is the striated character of the muscular tissue. The presence of two pairs of legs in the larva, however, is sufficient to confirm the view that they are aberrant Arthropods, while leaving it uncertain in what class they find their nearest allies. They have here been treated, together with the Pycnogonida, in an appendix to the Arachnida. As to the affinities of the Onychophora the view is now widely held that the members of this group can either be described as highly aberrant Arthropods or as highly modified Annelida. There is, according to this view, no justification

to regard them as ancestral forms connecting the Annelida with the Arthropoda. The Tardigrada are still more aberrant in some respects. They differ from Arthropods in general in the absence of external segmentation in the adult state, in the simple unjointed character of the appendages, in the absence of striation in the muscular fibres, and in the absence of organs of respiration and circulation. It is impossible to place them in any of the great classes, and they are perhaps best looked upon as a special offset of the Arthropod tree.

SECTION IX

PHYLUM MOLLUSCA

THE Mollusca, like the Arthropoda, form one of the chief divisions of the animal kingdom, both as regards diversity of organization and number of genera and species. They are sharply distinguished from Arthropods by the absence of segmentation, and by having, as a rule, an exoskeleton in the form of a *shell*, usually external, sometimes internal. An enumeration of the Classes of the Phylum will serve to give some notion of its extent.

Class 1.—SOLENOGASTRES, including the worm-like *Chætoderma* and *Neomenia*.

Class 2.—PLACOPHORA (LORICATA), including the *Chitons*.

Class 3.—GASTROPODA, including the univalved *Shell-fish*, such as *Periwinkles*, *Whelks*, *Snails*, etc.

Class 4.—SCAPHOPODA, including the *Tooth-shells*.

Class 5.—BIVALVIA (PELECYPODA), including the bivalved *Shell-fish*, such as *Mussels*, *Cockles*, *Oysters*, etc.

Class 6.—CEPHALOPODA (SIPHONOPODA) including the *Cuttle-fishes*, *Squids*, *Octopods*, and *Nautili*.

CLASS I.—SOLENOGASTRES.

The Solenogastres are a small group of highly primitive Molluscs including five families with over forty genera, of which *Chætoderma* (Fig. 523), *Neomenia* (Fig. 524), and *Proneomenia* are most thoroughly known. They are distinguished by their worm-like body, sometimes elongated and narrow and capable of being coiled into a spiral, sometimes comparatively short and thick. In most instances there is little difference in external appearance between the anterior and posterior ends. In some species of *Chætoderma* (Fig. 523) alone is there in sexually mature specimens a "head," separated off from the body by a constriction, as well as a posterior cloacal region

FIG. 523.—**Chætoderma nitidulum.** *a.* anus; *m.* mouth. (From the *Cambridge Natural History.*)

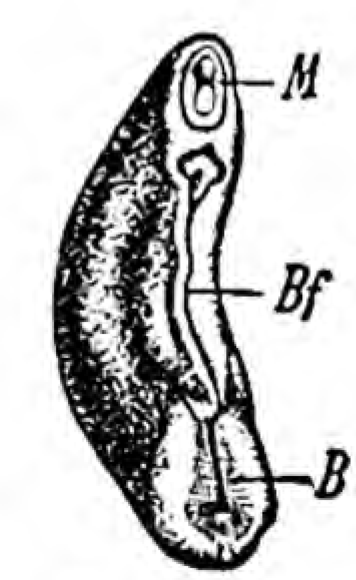


FIG. 524.—**Neomenia carinata.** *M.* mouth; *Bf.* ventral grove; *B.* cloaca with gill-folds. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Hansen.)

which is similarly marked off. A shell is completely absent. The body is generally almost completely covered by a cuticle enclosing spicules of calcified material. In many cases the dorsal surface is beset with uni- or multi-cellular epidermal papillæ. Along the middle of the ventral surface runs, in most instances, a groove in some cases merely represented by a narrow strip from which the cuticle and spicules are absent. This ventral groove, which is absent in Chætoderma, usually contains a slight, longitudinal, ciliated ridge, and is an organ of locomotion. With the ventral groove is connected in front an anterior ciliated groove, while behind it is in direct communication with the cavity

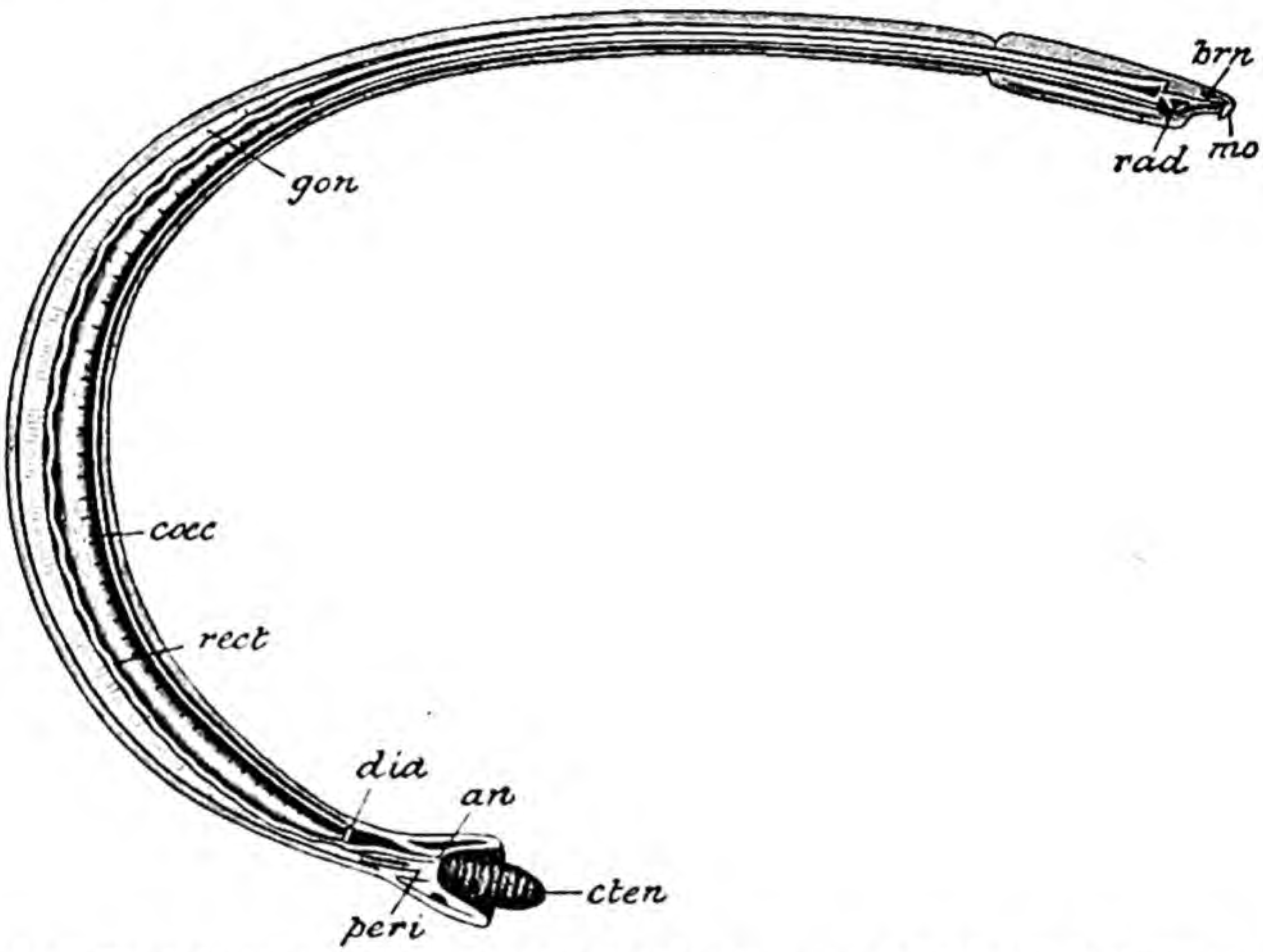


FIG. 525.—**Chætoderma nitidulum,** longitudinal section. *an.* anus; *brn.* brain; *cæc.* glandular cæca of mesenteron; *cten.* ctenidium; *dia.* diaphragm separating off the posterior portion of the body; *gon.* gonad; *mo.* mouth; *peri.* pericardium and heart; *rad.* radula; *rect.* rectum. (After Simroth.)

of the cloaca (*vide infra*). A ventral " foot "—an organ very highly developed in most Molluscs—is absent.

There is generally a cavity (*cloaca*) at the posterior end of the body into which the anus opens (Fig. 525). In a number of genera the cloaca contains either a pair or a circlet of gills (*ctenidia*) in the form of simple or complex folds of its wall. Gills are absent in Proneomenia.

Alimentary System.—The mouth is usually a longitudinal, rarely (*Chætoderma*) a transverse, slit, situated ventrally near the anterior extremity. There is a buccal cavity, with a rasping organ, the so-called *radula*[1] in

[1] For a description of the structure of this characteristic organ see the account of Triton (p. 551).

some cases (Fig. 525, *rad.*), and in others a single chitinous tooth supporting smaller denticles: sometimes teeth are entirely absent. There are both salivary and buccal glands. Very characteristic of the group as compared with other Molluscs is the presence of a straight intestine devoid of coils, and having connected with it a single dorsal cæcum and usually a double row of lateral cæca.

Body-cavity.—The interstices between the organs and the body-wall are filled with a form of connective-tissue with muscular fibres; a vertical diaphragm (Fig. 525, *dia.*) separates the posterior part of the body, containing the pericardium (*peri*), from the rest.

Vascular System.—The vascular system is very rudimentary. There is a

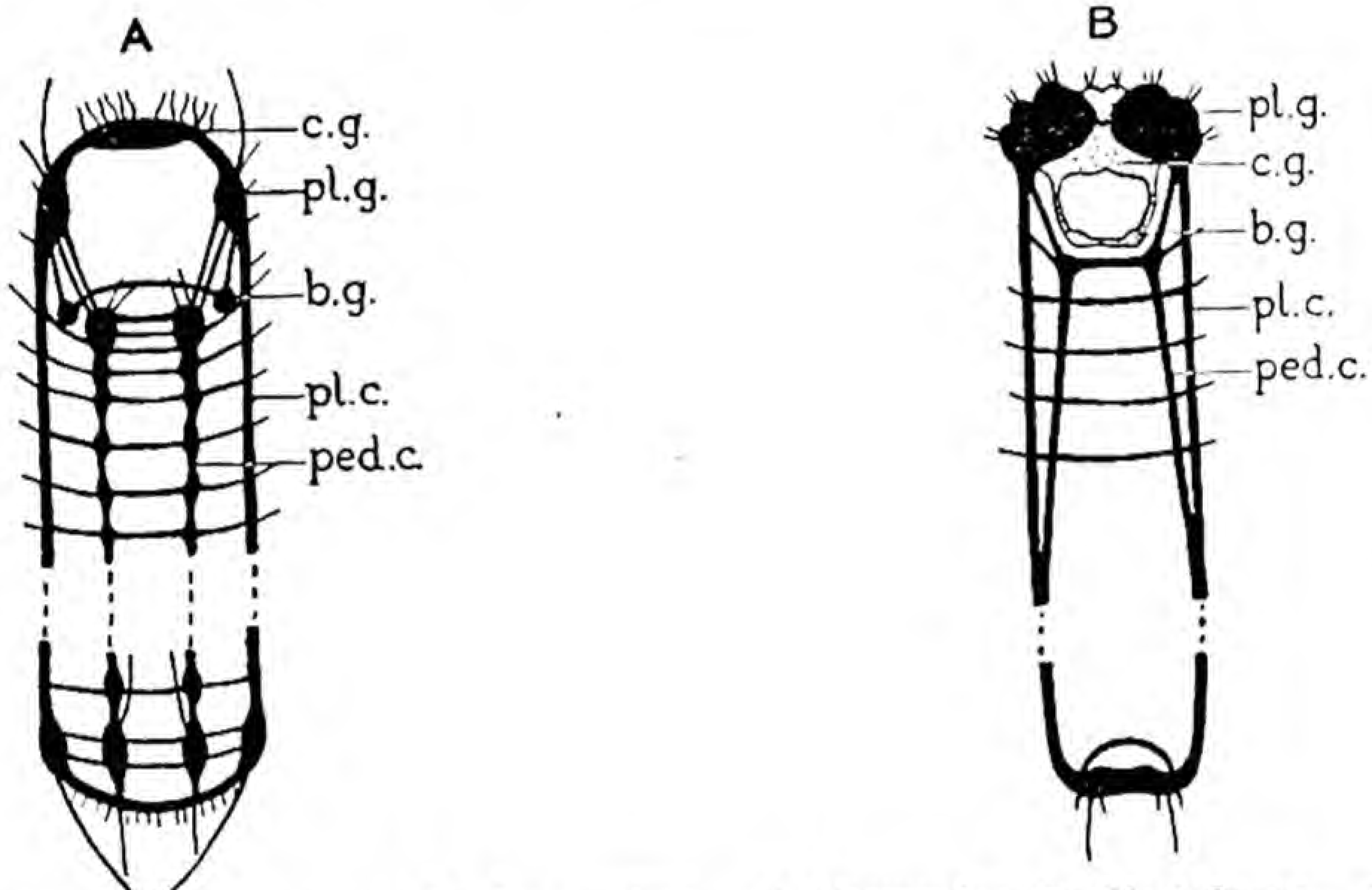


FIG. 526.—**Nervous systems of Solenogastres.** *A*, *Neomenia*; *B*, *Chætoderma*. *a. g.* anterior swelling of pleural cord; *b. g.* buccal ganglion; *c. g.* cerebral ganglion; *ped. c.* pedal cord; *pl. c.* pleural cord. (After Thiele.)

heart enclosed in a pericardium (Figs. 525 and 527, *peri*) and composed, when best developed, of an auricle and a ventricle.

The **Nervous System** (Fig. 526) consists of four longitudinal nerve-cords—two *pedal* and two *pleural*. These are connected together by an œsophageal ring, thickened dorsally into a single or double *cerebral ganglion* (*c. g.*); and in front of this is a second, more slender *buccal* (*stomatogastric*) nerve-ring with small ganglia (*b. g.*). The pedal cords (*ped. c.*) may present in front a pair of ganglionic thickenings connected by a commissure, and farther back there may be a series of enlargements united by commissures. The pleural cords (*pl. c.*), which are more or less enlarged in front into ganglionic swellings (*g. a.*) are connected behind, above the rectum, by a commissure which usually bears a median enlargement. Sometimes a union takes place posteriorly between

the cords of the two pairs. There are no eyes, or statocysts, or tentacles. The dorsal epidermal papillæ are perhaps sensory. Some have a sensory frontal lobe and a sensory pit or elevation in the middle line of the dorsal surface near the posterior end.

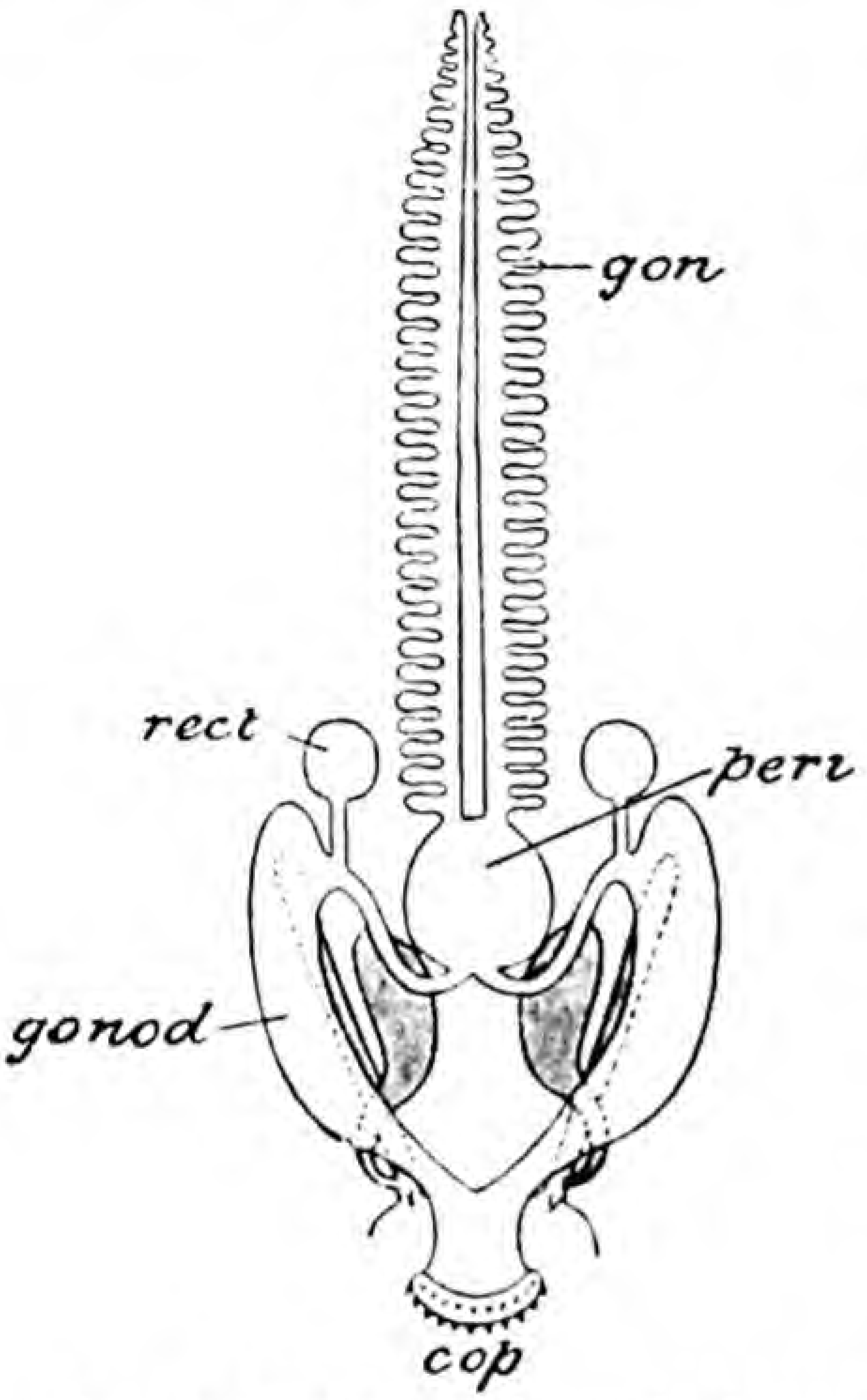


FIG. 527.—**Neomenia carinata,** reproductive organs. *cop.* copulatory organs; *gon.* gonads enclosed in extensions of the pericardial cavity; *gonod.* gonoducts; *peri.* pericardium; *rect.* receptaculum seminis. (From Simroth, after Wiren.)

Reproductive and Renal Organs.—With the exception of Chætoderma the Solenogastres are hermaphrodite. The gonads are generally paired (Fig. 527), in Chætoderma they are fused into a single one. The sexual products pass into the pericardial cavity and thence are carried to the exterior by a pair of ducts (cœlomoducts) opening into the cloaca. Renal organs are unknown.

Little is known of the **development** of the Solenogastres. The egg undergoes complete cleavage and gives rise to a gastrula by invagination. This develops into a form of *trochophore* with a ciliated ring, the *prototroch.* There is a metamorphosis which somewhat recalls the metamorphosis of the Nemertini. For a time the larva is provided with calcareous plates which are replaced later by the calcareous spicules mentioned above.

Modes of Life and Distribution.—The Solenogastres are marine animals of almost universal distribution, occurring at all depths They are absent from the littoral zone. Some of them burrow in the mud, others live in association with various colonial Cœlenterates, some appear to be free-living and predatory. There are no fossil records of Solenogastres.

CLASS II.—PLACOPHORA (LORICATA).

The Placophora are a class of marine Mollusca formerly included with the Solenogastres in the class Amphineura. They are, however, sufficiently far removed from the Solenogastres as to require inclusion in a distinct class. They comprise the *Chitons* (Fig. 528).

External Features.—In *Chiton* (Figs. 528 and 529) the body is dorso-ventrally compressed, convex above, and presents below a broad flat foot (narrow in *Chitonellus*) which acts not only as an organ for effecting creeping movements,

but also as a sucker for enabling the animal when at rest to adhere firmly, like a Limpet, to the surface of a rock. The head region is not distinctly separated

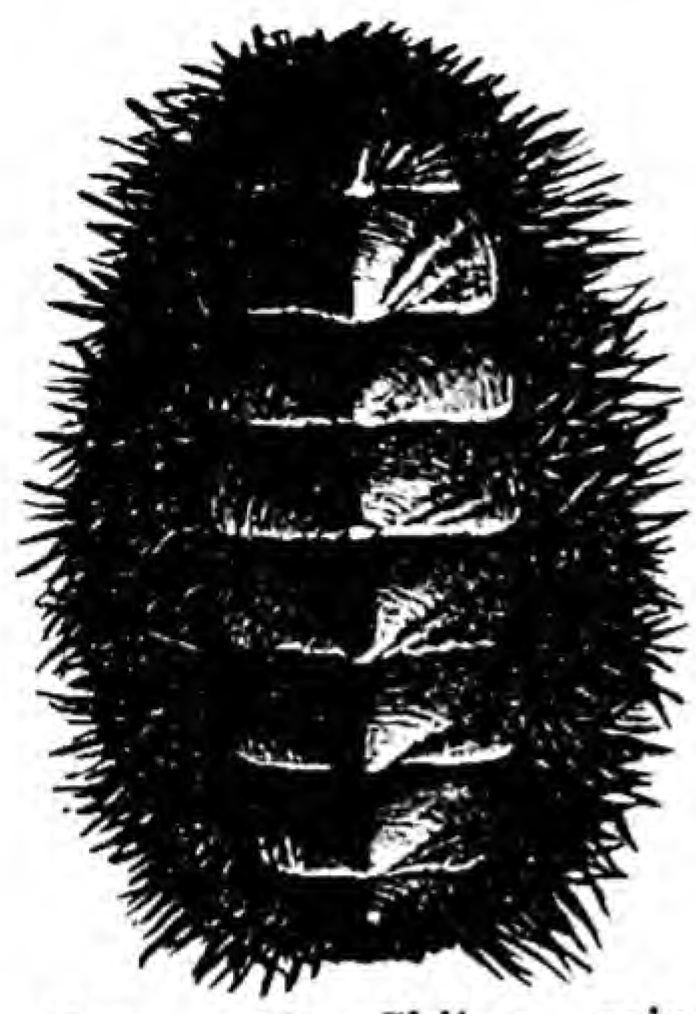


FIG. 528.—**Chiton spinosus,** dorsal view. (From the *Cambridge Natural History*.)

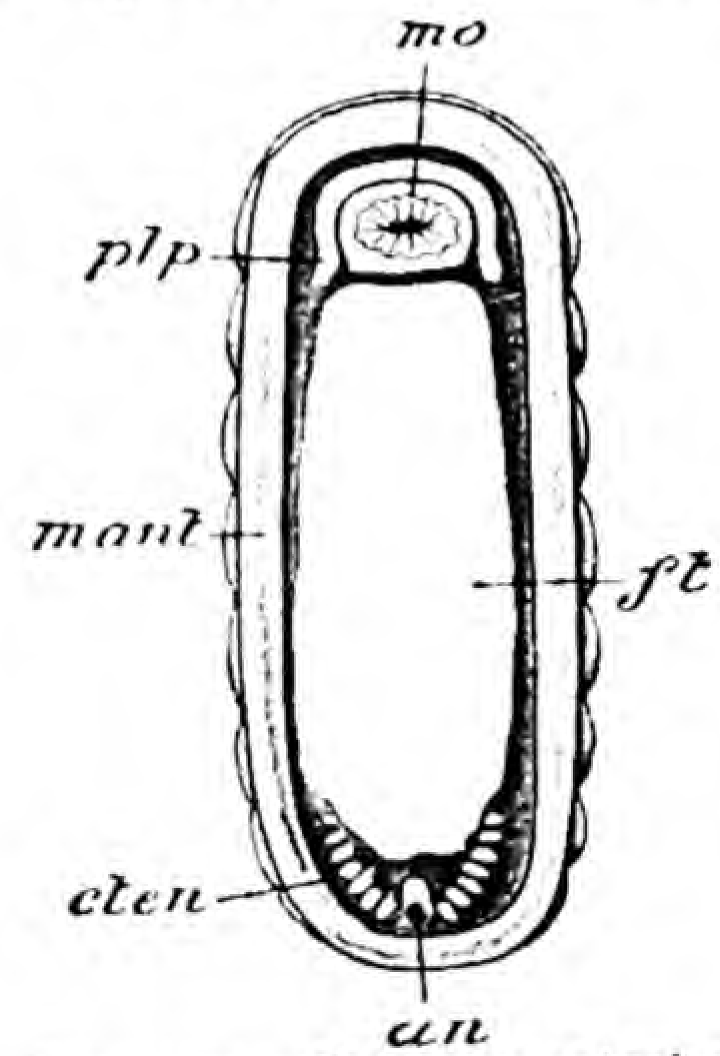


FIG. 529.—**Chiton,** ventral view. *an.* anus; *cten.* ctenidia; *ft.* foot; *mant.* mantle edge; *mo.* mouth; *plp.* palp. (After Pelseneer.)

off, and is not provided with eyes or tentacles. The most remarkable external feature of Chiton is the presence on the dorsal surface of a calcareous shell (Figs. 528 and 530) made up of no fewer than eight transversely elongated pieces or valves, arranged in a longitudinal row, articulating together and partly overlapping one another. They are sometimes partly, sometimes completely, covered over by a fold of the dorsal integument, which in the Placophora as in the rest of the Molluscs is called a *mantle.* Each valve consists of two very distinct layers, a more superficial and a deeper, the latter formed of compact calcareous substance, the former perforated by numerous vertical canals for the lodgment of the sense-organs to be presently referred to. Peripherally to the valves the mantle of Chiton and its allies is usually beset with a number of horny or calcified tubercles and spicules. The mantle develops only very slight lateral flaps, and under cover of these, in mere grooves which represent the mantle-cavities of other Molluscs, are a series of small gills (*ctenidia*) (Figs. 529 and 534, *cten.*) to the number of from fourteen to eighty. The mouth and anus are both median, situated at the anterior and posterior extremities respectively.

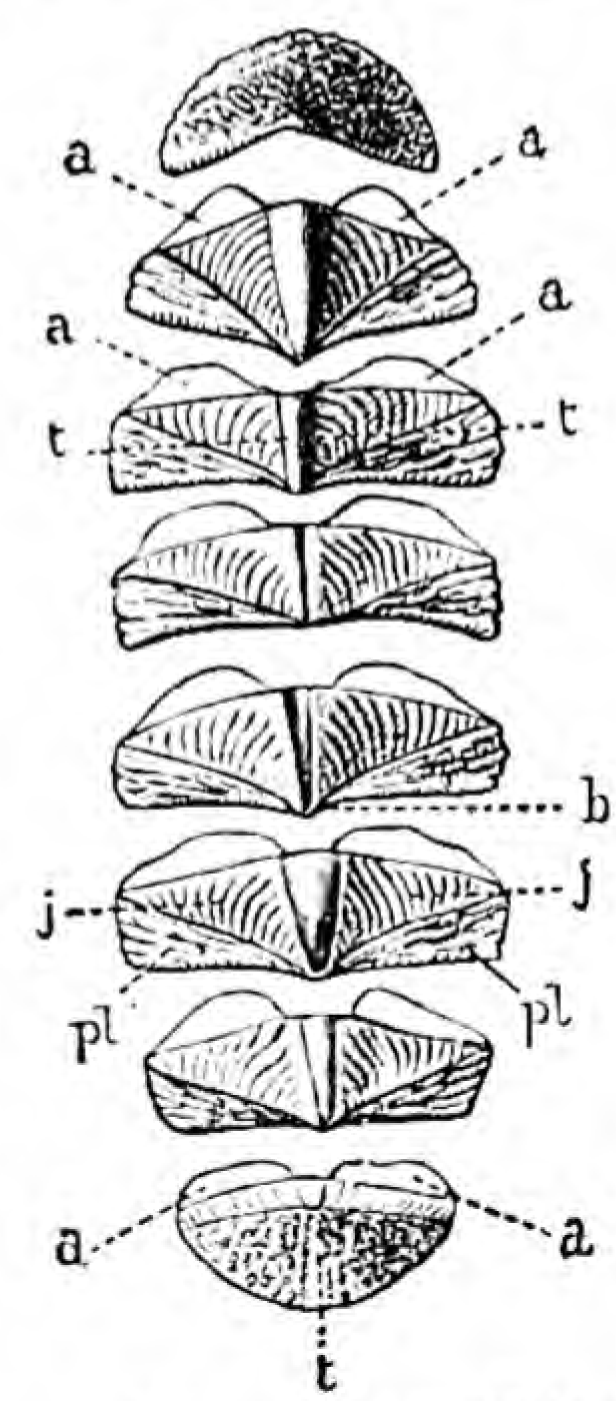


FIG. 530. — **Chiton,** valves of shell. (From the *Cambridge Natural History*.)

Alimentary System.—The buccal cavity always contains a muscular

elevation, the *odontophore* with a well-developed horny rasping organ, the *radula* (*vide*, p. 551). The intestine is elongated and coiled. There are salivary glands and a large paired liver (Fig. 531, *liv.*)

Body-cavity.—The cœlome is an extensive cavity, lined with a cœlomic epithelium, and divided into three *completely separated* parts—the pericardium, the genital cavity, and the general body-cavity.

Vascular System.—There is a well-developed heart (Fig. 531, *ht.*) consisting of a median ventricle and two lateral auricles. The pericardial cavity in which it lies is a space of considerable extent in the posterior region of the body, below the two last valves of the shell.

Nervous System.—There is an œsophageal nerve-ring consisting of a

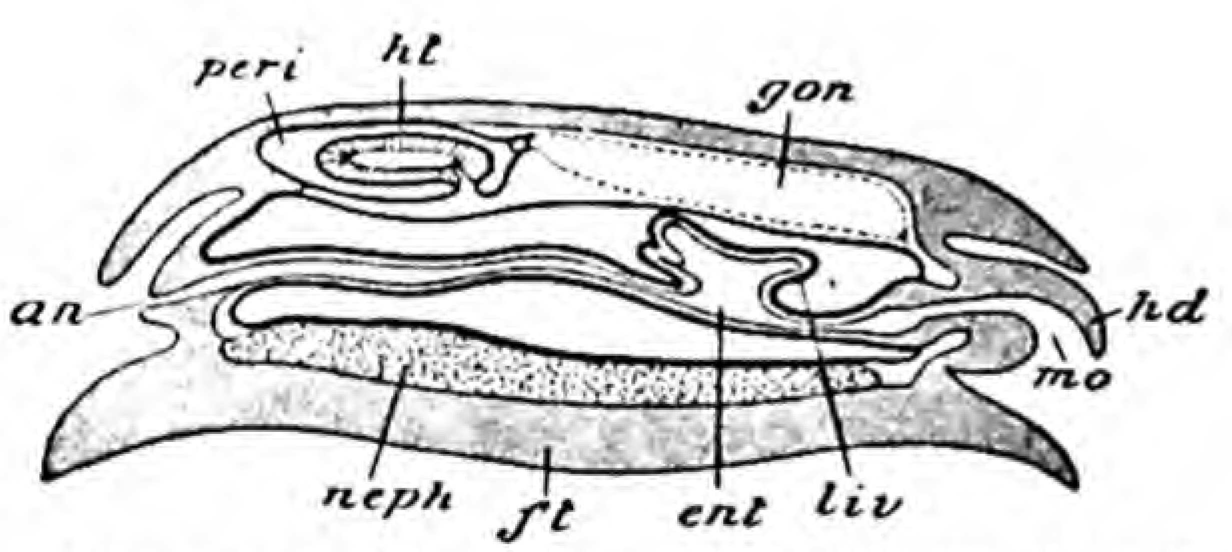


FIG. 531.—Diagrammatic longitudinal section of **Chiton**, specially intended to show the relations of the parts of the cœlome, which, except the genital parts, are bordered with a thick line. There is no communication between gonad and pericardium. *an.* anus; *ent.* enteric cavity; *ft.* foot; *gon.* gonad; *hd.* head-lobes; *ht.* heart; *liv.* liver; *mo.* mouth; *neph.* kidney; *peri.* pericardial cavity. (From Simroth, after Haller.)

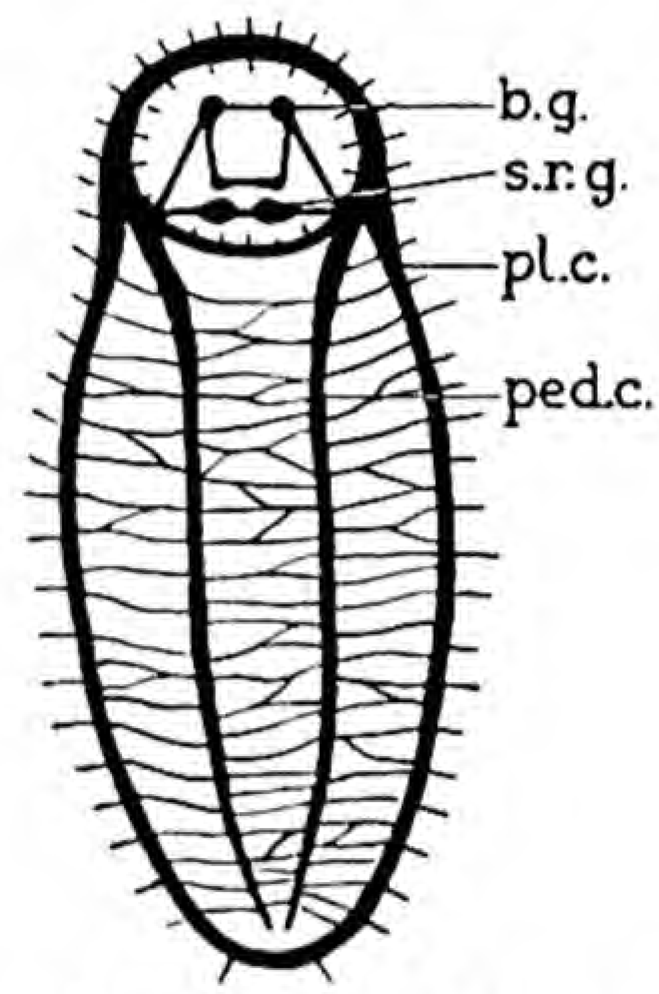


FIG. 532.—**Nervous system of Chiton.** *b. g.* buccal ganglion; *ped. c.* pedal cord; *pl. c.* pleural cord; *s. r. g.* sub-radular ganglion. (After Thiele.)

thicker dorsal *cerebral* portion not differentiated into ganglia, and a thinner ventral commissure (Fig. 532). The cerebral part sends off nerves to the labial palps, the lips, and to the buccal nerve-ring with its ganglionic swellings (*b. g.*). The ventral commissure gives off connectives to the sub-radular ganglia (*s. r. g.*). Two pairs of longitudinal nerve-cords, *pedal* and *pleural*, are given off posteriorly: the former, from which arise nerves to the foot, are joined by numerous commissures passing beneath the enteric canal; the latter, which send off nerves chiefly to the mantle and the ctenidia, are united together by a supraretal commissure at the posterior end of the body. The large cords contain nerve-cells throughout their length.

The conspicuous **sense-organs** present on the head of Gastropods (*vide infra*), are absent in the Placophora. A pair of processes situated in

front, at the sides of the mouth, have the character of labial palps. In the buccal cavity there are cup-shaped *gustatory organs* supplied with nerves from the cerebral commissure, and in front of the odontophore is a thickening of the epithelium—the *subradular organ*—containing nerve-endings. Remarkable sensory organs, the *æsthetes* and the *micræsthetes*, lie in the canals already mentioned as occurring in the superficial layer of the shell-valves. The æsthetes may take the form of eyes, with cornea, lens, pigment-layer, iris, and retina (Fig. 533); in some cases the lens is absent.

Reproductive and Renal Organs.—The sexes are distinct. The testis

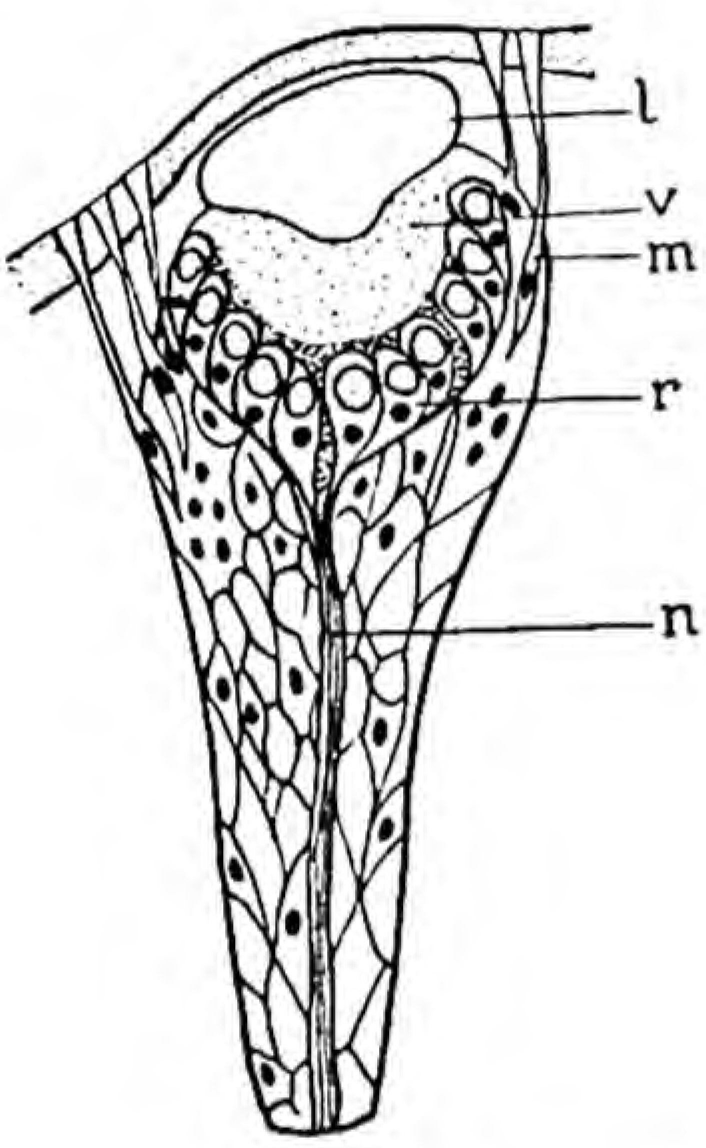


FIG. 533.—**Æsthete-eye** of a Chitonid (*Acanthopleura japonica*). *l.* lens; *m.* micræsthete; *n.* nerve-processes; *r.* retina-cell; *v.* vitreous body. (After Nowikoff.)

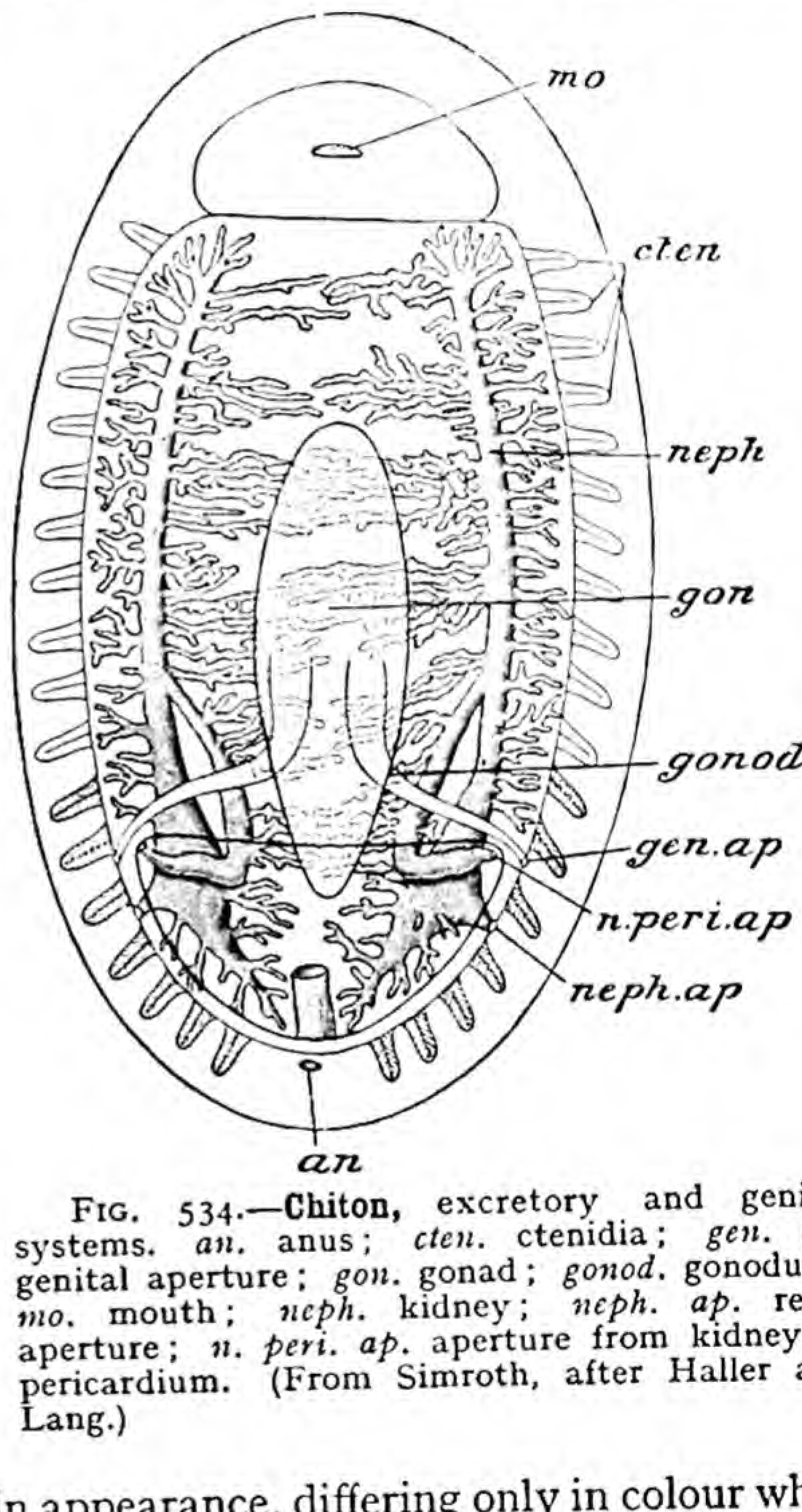


FIG. 534.—**Chiton,** excretory and genital systems. *an.* anus; *cten.* ctenidia; *gen. ap.* genital aperture; *gon.* gonad; *gonod.* gonoduct; *mo.* mouth; *neph.* kidney; *neph. ap.* renal aperture; *n. peri. ap.* aperture from kidney to pericardium. (From Simroth, after Haller and Lang.)

and ovary (Fig. 534, *gon.*) are similar in appearance, differing only in colour when the sexual products are mature. Each is an unpaired sac marked by a series of slight lateral constrictions. There are two gonoducts (*gonod.*). Two symmetrical kidneys open internally into the pericardium by a ciliated funnel-like opening (*n. peri. ap.*) and externally (*neph. ap.*) between two of the posterior ctenidia some little distance in front of the anus and behind the genital apertures (*gen. ap.*). Each consists of a looped main tube, into which open numerous minute tubules which ramify among the viscera.

Development.—The eggs of Chiton are fertilized in the mantle-cavity,

where in one species they are retained until the embryos are fully developed. In other cases they are laid singly or in strings. The cleavage is complete, and corresponds very closely with that of the Polychæta (p. 319). The four macromeres give off three quartettes of micromeres, which give rise to the ectoderm. The macromeres give origin to the endoderm, and the mesoderm originates in a cell given off by the posterior macromere. Micromeres and macromeres at first arrange themselves in such a way as to form a somewhat flattened blastula, one side of which (vegetative pole) is composed of a comparatively small number of large endoderm cells. Then follows the invagination of the cells of the vegetative side and the resulting formation of a gastrula: this soon becomes elongated in the direction of the future long axis.

Two rings of cells surrounding the embryo develop cilia (Fig. 535, *cil.*), and

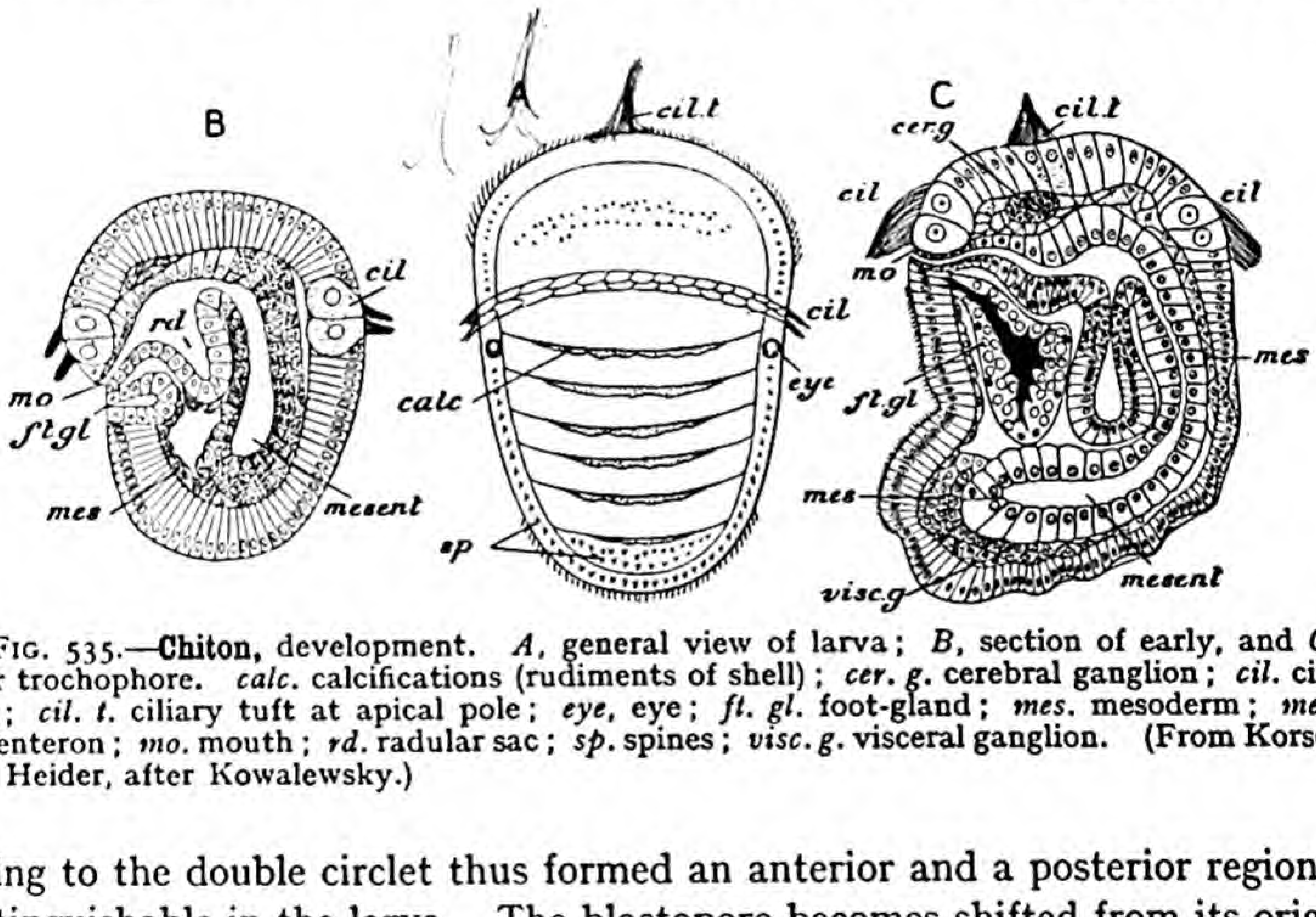


FIG. 535.—**Chiton,** development. *A*, general view of larva; *B*, section of early, and *C*, of later trochophore. *calc.* calcifications (rudiments of shell); *cer. g.* cerebral ganglion; *cil.* ciliary ring; *cil. t.* ciliary tuft at apical pole; *eye*, eye; *ft. gl.* foot-gland; *mes.* mesoderm; *mesent.* mesenteron; *mo.* mouth; *rd.* radular sac; *sp.* spines; *visc. g.* visceral ganglion. (From Korschelt and Heider, after Kowalewsky.)

owing to the double circlet thus formed an anterior and a posterior region are distinguishable in the larva. The blastopore becomes shifted from its original posterior position forwards on the ventral surface until it comes to be situated just behind the circlet of cilia; it undergoes elongation, and an invagination of ectoderm round its anterior end forms the mouth (*mo.*) and stomodæum. A ventral diverticulum of this forms the rudiment of the radular sac (*rd.*). By greater relative growth of the postoral part the embryo assumes the form of a pear; and in this *trochophore* stage, with a pre-oral circlet and a bunch of cilia in the middle of the apical area, it becomes free in the case of certain of the species, while in others it remains enclosed in the egg up to a later stage of development. As yet there is no anus, that aperture, with the proctodæum, being formed later by invagination. An apical plate is not present in the early larva; but the rudiments of the cerebral ganglia (*C*, *cer. g.*), which sub-

sequently appear at the apical pole, probably represent it. Primitive nephridia, such as occur in annelidan and many molluscan trochophores, are not present.

The post-oral region now becomes greatly elongated; the mesoderm increases greatly in extent, and forms two well-defined streaks, which are afterwards divided into parietal and visceral layers with a cœlomic space between them. The post-oral part of the embryo now presents an appearance resembling rudimentary segmentation. This is due to the development of a series of rudiments of the eight pieces of the shell (*A*, *calc.*), each of which is formed independently after the fashion of the entire shell of other Mollusca.

Mode of Life and Distribution.—The Placophora are all marine and occur at all depths, though most abundant on the shore between tidal limits. They are all vegetable feeders, their food consisting of minute Algæ and Diatoms. When at rest, they adhere firmly to the surface of a rock or a block of coral by means of the sucker-like foot. When forcibly detached the animal curls itself up into a ball, and will only after a considerable time slowly extend itself again: all its movements are extremely sluggish.

Numerous fossil Placophora are known from the Ordovician onwards. The valves of the Palæozoic genera differ from those of most recent forms in the absence of the articulations.

CLASS III.—GASTROPODA.

The Gastropoda, including the Snails and Slugs, Limpets, Whelks, Periwinkles, Sea-hares, and the like, are Mollusca in which there is, as a rule, a shell composed of a single piece. The body is inequilateral, owing to one-sided development. There is a well-developed ventral foot, usually with a broad, flat surface on which the animal creeps. A head-region bearing eyes and tentacles is distinguishable in front of the foot. The majority of the families of Gastropoda are marine, a few of these being pelagic; but some inhabit fresh-water, and others are terrestrial.

1. Example of the Class.—The Triton (*Triton rubicundus*).[1]

Triton is a marine Gastropod living in shallow water, usually close inshore. The species to which the following description specially applies has a very wide range, from the English Channel to the South Pacific, and occurs as a fossil as far back as the Miocene. In many respects the English Whelk (*Buccinum undatum*) will be found to conform to the description.

The shell (Fig. 536) is a very hard and dense calcareous structure, and has the form of an elongated hollow cone closely wound round a central axis. The apex of the cone is the organic apex of the shell, and is the point from which the growth of the shell has proceeded: the base is represented by the wide

[1] Or *Charonia rubicunda*.

oblique opening—the *mouth* or *peristome* of the shell. Starting from the apex along the internal cavity of the spirally-wound cone, in order to reach the mouth in an adult shell, we pass completely round the central axis five times—*i.e.*, the spiral consists of five turns. In following the turns, the direction taken is to the right, that is to say, the spiral of the shell is a right-handed or *dextral* one. The axis (Fig. 537) is in the shape of a twisted shelly rod—the *columella*—containing a narrow lumen; it is formed by the close union of the axial portions

FIG. 536.—Shell of **Triton rubicundus.** Natural size.

FIG. 537.—Longitudinal median section of the shell of **Triton rubicundus.**

of the wall of the spiral. The windings of the spiral are marked on the outer surface of the shell by a narrow impressed spiral line or *suture*, parallel with which are numerous fine ridges and depressions—the *lines of growth*; the increase in size of the shell takes place in the direction of these lines. At certain points, usually three in a full-grown shell, the spiral is interrupted by a transversely directed edge which appears to overlap the succeeding portion; this edge marks the position which the mouth of the shell has occupied during regularly recurring periods of arrest of growth, probably annual.

The mouth of the shell is bordered on the side turned away from the

columella by a prominent rim or *outer lip* and on the opposite side by the smooth *inner lip* of the peristome. The outer lip is in relation to the dorsal surface of the body of the animal, the inner lips in relation to the ventral surface. A siphonal process of the outer lip protects the *siphon*, a spout-like process of the edge of the mantle.

When removed from the water, or disturbed in any other way, the animal becomes completely withdrawn into the interior of the shell, when the latter is observed to become closed by a plate—the *operculum* (Fig. 538)—which fits accurately across the passage some distance internal to the peristome. The operculum is an oval plate of chitinoid material hardened by calcareous deposits; like the shell itself, it exhibits lines of growth marking what has been its edge at successive stages in the development of the shell.

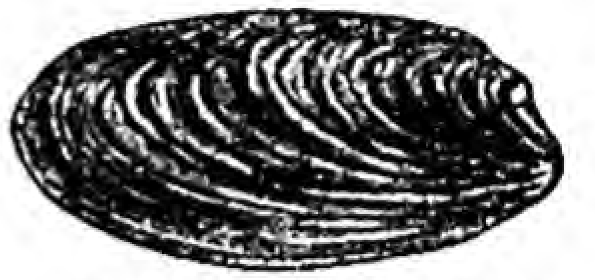


FIG. 538.—Operculum of **Triton rubicundus.**

The minute structure of the shell is in the main similar to that of the fresh-water Mussel (*vide infra*, Fig. 581, p. 583). Its outer surface is covered with a thin layer of uncalcified chitinoid material, the *periostracum*, beneath which is a thick *prismatic* layer (*mother-of-pearl*), and, lining the inner surface, a layer of *nacre* both consisting of calcium carbonate.

External Features of Soft Parts.—The Triton is able to extend itself to a

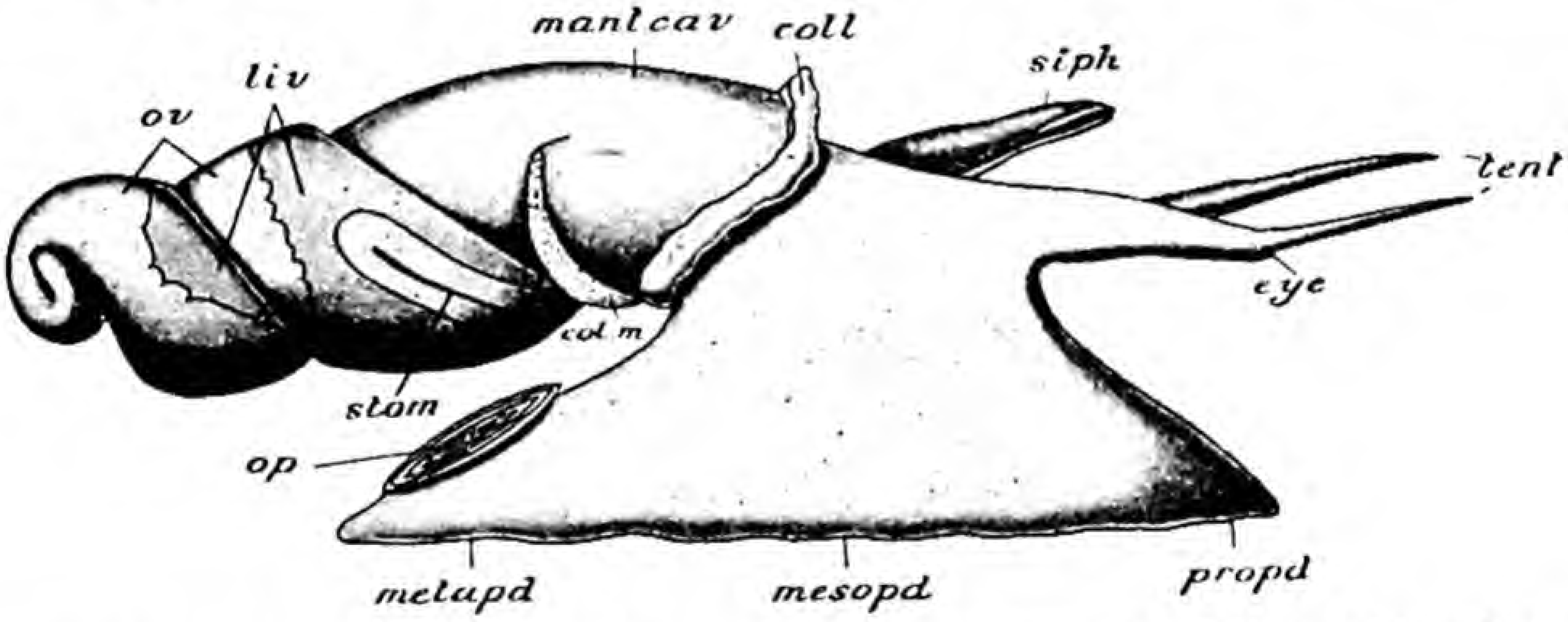


FIG. 539.—Lateral view of the body of a female specimen of **Triton rubicundus**, removed from the shell, moderately extended. *col. m.* columellar muscle; *coll.* collar of mantle; *eye*, eye; *liv.* liver; *mant. cav.* mantle-cavity; *meso.* mesopodium; *op.* operculum; *ov.* ovary; *prop.* propodium; *siph.* siphon; *stom.* stomach; *tent.* tentacles.

considerable degree beyond the mouth of the shell; but a portion of the body always remains concealed in the interior, even when the animal has extended itself to its utmost, the body being, like that of nearly all the Mollusca, organically connected with the shell. In Triton the connection is by means of a strong muscle—the *columellar muscle* (Fig. 539, *col. m.*)—which extends from the concave right side of the animal to the columella, into which it is inserted; it is by means of this muscle that the anterior portion of the body, capable of being thrust out through the mouth of the shell, may again be withdrawn.

If the Triton be examined in the extended condition (Fig. 539) it will be found to present a distinct head, which bears dorsally a pair of appendages —the *tentacles* (*tent.*)—of a sub-cylindrical shape, slightly compressed towards their bases, and narrowing somewhat towards their free extremities; these are capable of being extended and contracted, but not of being completely retracted. Each bears on its outer side, some little distance from the base, a prominent *eye* (Fig. 546). At the anterior end of the head on its ventral aspect is the opening of the mouth. When the animal is feeding, an elongated cylindrical *introvert* (Fig. 540), comparable to that of Sipunculus (p. 380), is extended forwards, bearing the mouth at its anterior end; at other times the introvert is completely involuted within the head and anterior portion of the body. In the male, on the right-hand side of the body some little distance behind the head, is a long, narrow, fleshy process, broader at the base than at the free end, and deeply grooved longitudinally; this is the *penis*. Running back from its base is a narrow groove with prominent lips—the *sperm-groove*, continuous with that of the penis; in the female these parts are not represented.

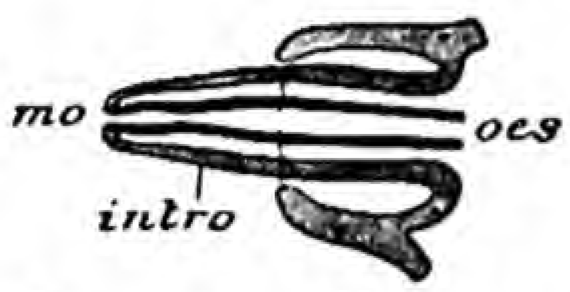


FIG. 540.—Diagram of the introvert of **Triton**, in longitudinal section, as it appears when almost completely extended. The black lines represent the wall of the alimentary canal; the cross-hatched part the wall of the introvert; the dotted line marks the position of the opening through which the introvert passes. *intro.* introvert; *mo.* mouth; *oes.* lumen of œsophagus.

Foot.—On the ventral side of the body which the animal applies to the surface of the ground when it extends from the shell is a flat surface elongated in the antero-posterior direction. The wall of the body in this region is composed of a dense mass of muscular fibres: this is the principal part of the foot (*propodium* and *mesopodium* combined); the posterior portion (*metapodium*) is a thick process projecting behind this and bearing the operculum on its surface (Fig. 539, *op.*). The foot is highly contractile, and it is by means of contractions passing over it in a succession of undulations that the animal creeps along, dragging after it the rest of the body enclosed in the shell. In the middle line of its flat surface, nearer the anterior than the posterior end, is a slit-like aperture leading into a cavity lined with unicellular glands—the *pedal gland*.

When the remainder of the body has been removed from the shell, it is found to be twisted up into a coil—the **visceral spiral,** corresponding to the spire of the shell within which it was lodged. This is unsymmetrical, the axis of the spiral being directed not straight backwards, but backwards, upwards, and to the right. The external asymmetry of the body is not strongly marked in the part which is capable of being protruded from the shell, but is still recognizable; and an examination of the internal organs shows a marked excess of development on the left-hand side. The surface of the part of the animal which is capable of being pushed out from the shell is covered with a thick

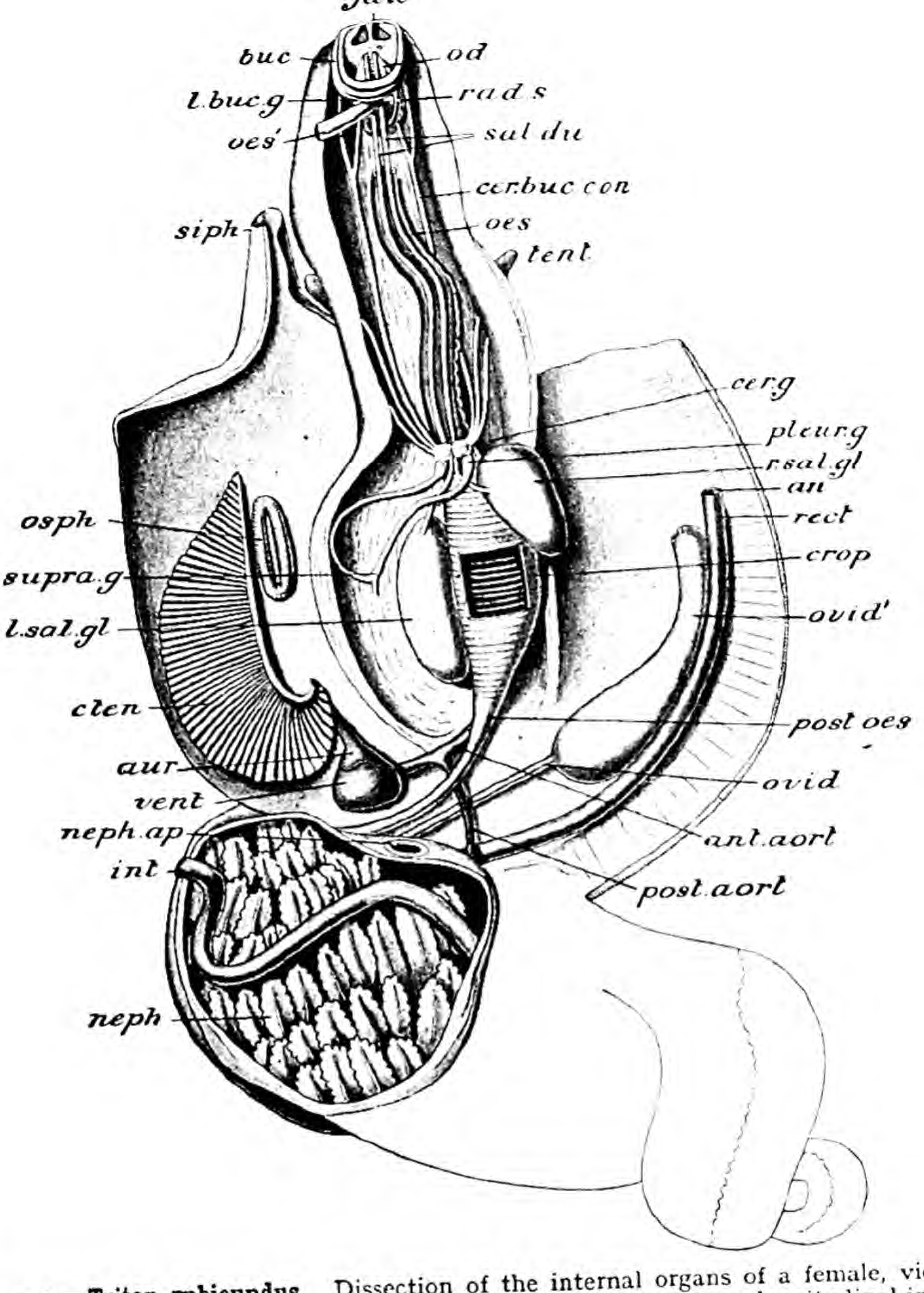


FIG. 541.—**Triton rubicundus.** Dissection of the internal organs of a female, viewed from the dorsal side. The roof of the mantle-cavity has been divided by a longitudinal incision and the flaps laid out, that on the left bearing the ctenidium and osphradium, and that on the right the rectum and terminal part of the oviduct. The muscular dorsal wall of the body and the introvert have been divided so as to bring into view the anterior part of the alimentary canal and a portion of the nervous system. The buccal cavity has been tilted up and opened so as to show the odontophore, and the œsophagus has been cut through near the anterior end. A portion of the ventral wall of the crop has been removed so as to bring the internal folds into view, and the interior of the kidney with the contained portion of the intestine has been exposed. *Note.*—The complete course of the intestine through the kidney is not shown; the stomach is not seen, being hidden by the kidney, and the ovary is not represented. *an.* anus; *ant. aort.* anterior aorta; *aur.* auricle; *buc.* buccal cavity; *cer. buc. con.* cerebro-buccal connective; *cer. g.* cerebral ganglia; *crop*, crop; *cten.* ctenidium; *int.* intestine; *jaw*, jaw; *l. buc. g.* left buccal ganglion; *l. sal. gl.* left salivary gland; *neph.* kidney; *neph. ap.* renal aperture; *od.* odontophore; *oes.* œsophagus; *oes'.* anterior end of same, cut and turned aside; *osph.* osphradium; *ovid.* oviduct; *ovid'.* terminal thick-walled portion of oviduct; *pleur. g.* pleural ganglion; *post. aort.* posterior aorta; *post. oes.* posterior œsophagus; *rad. s.* radula sac; *rect.* rectum; *r. sal. gl.* right salivary gland; *sal. du.* salivary duct; *s ph.* siphon; *supra. g.* supra-intestinal parietal ganglion; *tent.* tentacle; *vent.* ventricle.

integument, which is darkly pigmented except on the lower surface of the foot. Over the visceral spiral the **mantle** forms a thin, delicate, colourless layer. Anteriorly the mantle becomes thickened and pigmented, and at the posterior limit of the protrusible part gives rise to a thickened ridge, the *collar* (Fig. 539, *coll.*), forming a semicircle over the dorsal and lateral regions. In the middle the collar is not in close contact with the body, but leaves a large cleft leading into a very wide space extending backwards for a considerable distance. This space, which is formed by an infolding of the mantle, is termed the *mantle-* or *pallial-cavity*. In it are to be found the *ctenidium*, the *osphradium*—a typical molluscan sense-organ—and the anal, excretory, and reproductive apertures. The wall of the cavity is much folded and plaited, and contains a quantity of glandular tissue, the plaits being most numerous on the right-hand side in front of the anus.

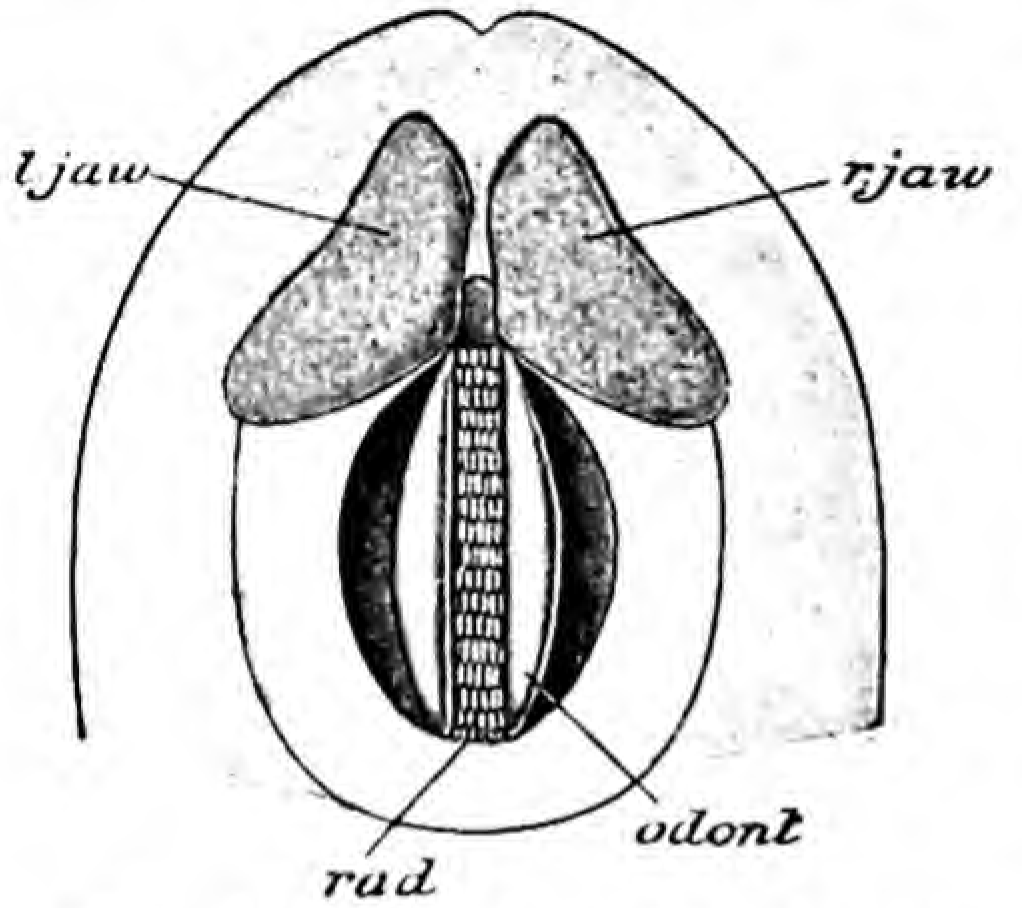


FIG. 542.—**Triton rubicundus.** Interior of the buccal mass, from above, magnified. *l. jaw*, left jaw; *odont.* lateral surface of odontophore; *rad.* radula; *r. jaw*, right jaw.

The **ctenidium** or gill (Fig. 541, *cten.*) is closely applied to the wall of the mantle-cavity to the left of the middle. It consists of a main stem, in which are connected a row of delicate flexible laminæ set at right angles to it: these are broadest in the middle, becoming smaller towards the ends.

The **osphradium** (*osph.*) lies close to the ctenidium on its outer side, in the natural position of the parts (reversed in the figure owing to the reflection of the wall of the mantle-cavity). It presents a central axis, connected at right angles with which are two rows of close-set delicate lamellæ. Like the ctenidium, it is closely applied to the wall of the mantle-cavity throughout its length. The laminæ of the osphradium are supplied with nerves which ramify over them. It is an organ of the chemical sense, and its function seems to be to test the condition of the water that enters the mantle-cavity.

Digestive System.—The mouth, situated at the anterior end of the introvert, leads into a large chamber with muscular walls, the *buccal cavity* (*buc.*). At the sides of the entrance to this cavity the investing cuticle is thickened to form two distinct horny plates—the *jaws* (Figs. 541, 542, and 543, *jaw*). The jaws are flexible, and on examination under the microscope are found to be composed of numerous rows of minute bodies, the *denticles*; the anterior edge is minutely denticulated. From the floor of the cavity rises an elevation, the *odontophore* (Fig. 541, *od.*, Fig. 542, *odont.*), which is somewhat elongated in the direction of the long axis of the body and compressed laterally. Over the

summit of the odontophore runs longitudinally a narrow strap-like body, the *radula* or *lingual ribbon* (Figs. 542 and 543, *rad.*), beset with numerous minute horny teeth arranged in transverse rows. Posteriorly this toothed ribbon passes into a narrow curved pouch—the *radular sac* (Fig. 541, *rad. s.*, Fig. 543, *rad. sac.*)—extending backwards from the posterior and lower aspect of the buccal cavity. Anteriorly it does not extend beyond the odontophore-prominence. The latter contains cartilages (Fig. 543, *cart.*) serving for the support of the whole apparatus, and is capable of being extruded, with the radula which it bears, through the opening of the mouth, by the contraction of sets of protractor muscular fibres. Muscles inserted into the odontophore are also responsible for the movements of the radula by means of which it produces a rasping effect on the food; and probably the radula itself is capable of a certain degree of to-and-fro movement on the membrane (*sub-radular membrane*) which lies beneath it. The entire buccal cavity is capable of being

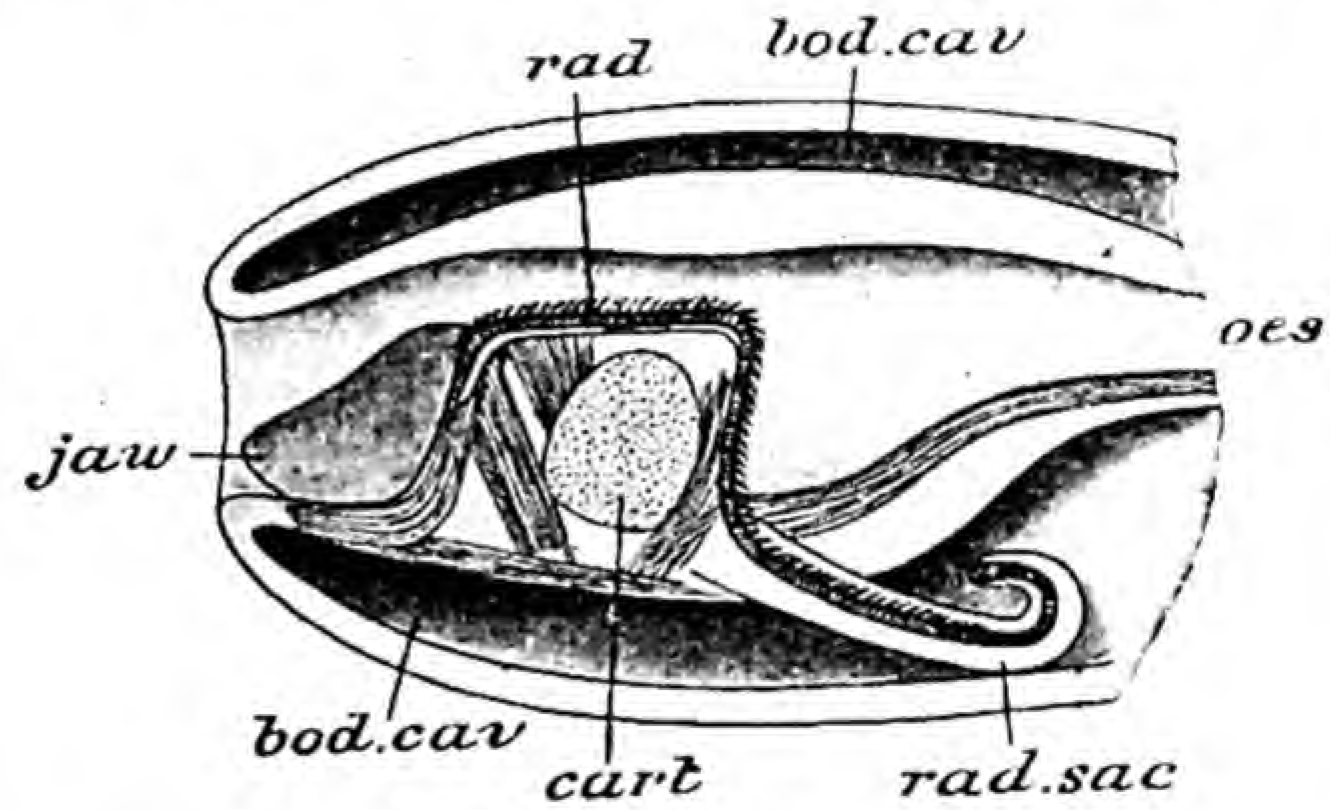


FIG. 543.—**Triton rubicundus.** Diagrammatic longitudinal vertical section of buccal cavity. *bod. cav.* body-cavity; *cart.* cartilage of odontophore; *jaw*, right jaw; *oes.* œsophagus; *rad.* radula; *rad. sac.* radula sac.

drawn forwards towards the mouth opening, or backwards into the introvert, by the contraction of strands of muscular fibres passing from its wall to the wall of the body.

From the buccal cavity runs backwards a long narrow tube with sacculated walls—the *œsophagus* (Figs. 541 and 543, *œs.*). Posteriorly this opens into a large ovoid sac—the *crop* (Fig. 541, *crop*). The outer surface of the crop appears marked with numerous close-set fine lines, transverse or oblique in direction; and, when the cavity of the organ is opened, it is found that these correspond to numerous delicate folds which extend far inwards, and almost completely block up the lumen. On either side of the crop is a large *salivary gland* (Fig. 541, *l. sal. gl.*, Fig. 545, *r. sal. gl.*)—partly composed of a compact glandular substance, partly of spongy tissue in which the secretion collects. The two salivary glands are unlike in size and shape, the left being much longer than the right. Each has a narrow duct (*sal. du.*) which runs forwards

and inwards to the dorsal surface of the œsophagus, where the two come into close apposition, becoming embedded in the wall of the œsophagus, along which they run forwards to open into the buccal cavity.

From the crop leads backwards and to the left a narrow cylindrical tube —the *posterior œsophagus*. On this follows a *stomach* (Fig. 539, *stom.*) which is in the form of a U-shaped tube partly embedded in the substance of the *digestive gland* or "*liver*," the *hepatic ducts* from which open into it. The tubular stomach is followed by a somewhat narrower tube—the *intestine* (Fig. 541, *int.*). This enters the cavity of the kidney, round the interior of which it bends; and, leaving it at its right-hand side, runs forwards in a straight course as the *rectum* (*rect.*), embedded in the glandular wall of the mantle-cavity, to near the anterior end, where it terminates in a short, freely projecting, spout-like portion, with the anus (*an.*) at its extremity.

The *digestive gland* or "*liver*" forms a mass of reddish-brown glandular follicles which compose the greater part of the bulk of the visceral coil.

Vascular System.—Close to the base of the ctenidium, behind it and a little to the right, is the *heart*, lodged in a cavity, the *pericardium*, lined by a transparent membrane—the *pericardial membrane*. The heart consists of two chambers, an auricle (Fig. 541, *aur.*) and a ventricle. The auricle, which is the smaller of the two, is situated somewhat in front of the ventricle, close to the ctenidium, from the main central vessel of which it receives the blood. The ventricle (*vent.*) is of somewhat pyramidal shape, but with the edges rounded off. Its wall is extremely thick and muscular. Passing out from the ventricle towards the right is a thick artery, which soon divides into two, one running forwards, the other backwards—the *anterior* (*ant. aort.*) and *posterior* (*post. aort.*) *aortæ*. The former is a very large trunk which runs forwards below the posterior œsophagus, crop, and anterior œsophagus, giving off branches to the region of the head as it goes. The posterior aorta, narrower than the anterior, passes into the visceral spiral, where it breaks up into branches for the supply of the various parts. The venous blood-system consists largely of sinuses devoid of proper epithelial walls. In these sinuses the blood is collected and conducted back to the auricle, passing on its way through the kidney, the gills, and the mantle.

Excretory System.—There is only one *kidney* (Fig. 541, *neph.*), a large organ situated dorsally, behind the pericardium. It is a sac with thick, glandular, and highly vascular walls, the inner surface of which is thrown into numerous complex folds. In front it communicates directly by a large aperture (*neph. ap.*) with the mantle-cavity, and by a narrow passage with the pericardium.

The **nervous system** (Figs. 544 and 545) consists of two pairs of nerve-ganglia—the *cerebral* (*cer. g.*) and the pleural (*pl. g.*)—lie close together over the posterior part of the œsophagus, just where it passes into the crop. The

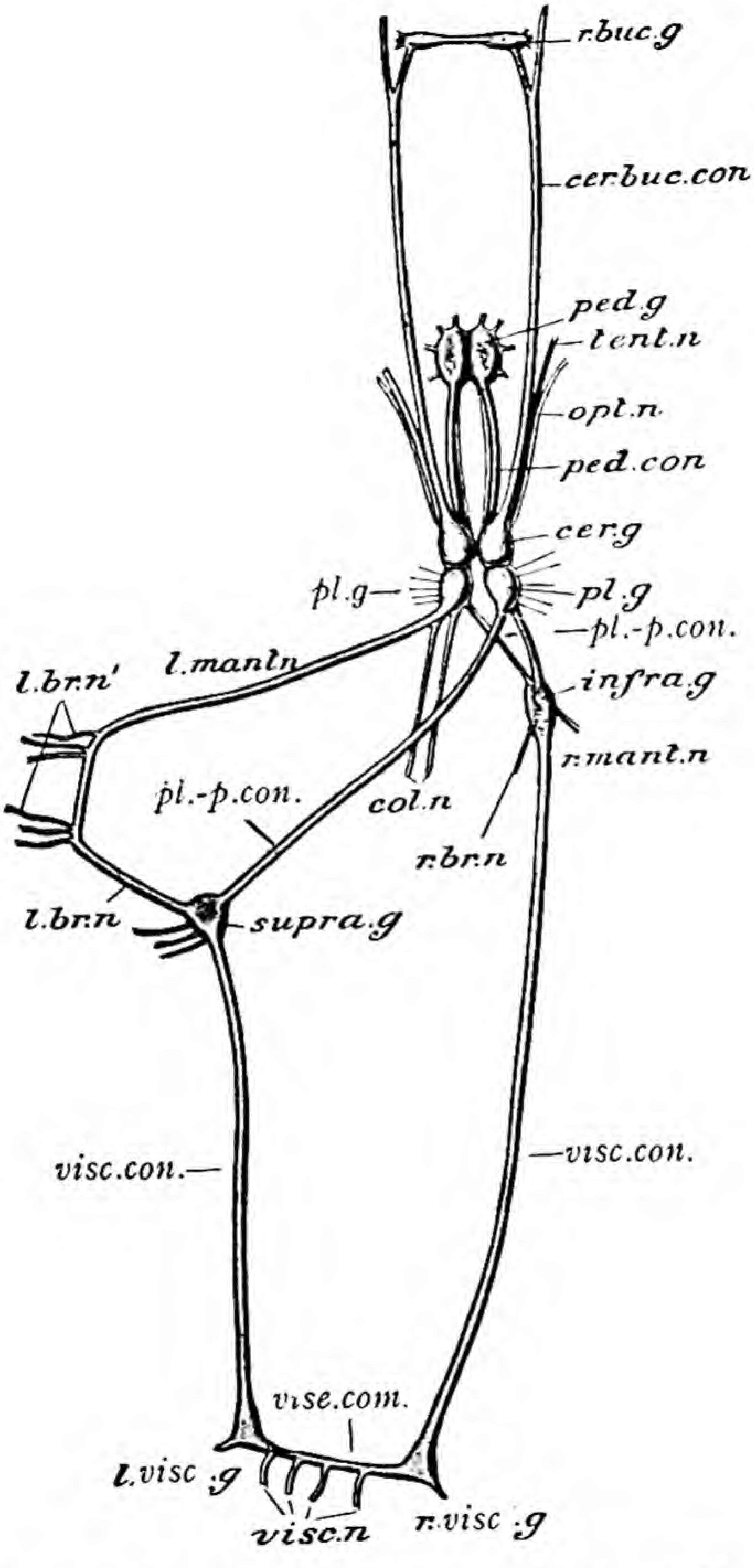


FIG. 544.—**Triton rubicundus.** Nervous system, from the dorsal side. *cer. buc. con.* cerebro-buccal connective; *cer. g.* cerebral ganglia; *col. n.* nerves to the columellar muscle; *infra. g.* infra-intestinal parietal ganglion; *l. visc. g.* left visceral ganglion; *l. br. n.* left branchial nerve; *l. br. n'.* nerves to branchia and osphradium; *l. mant. n.* left mantle-nerve; *opt. n.* optic nerve; *ped. con.* cerebro-pedal and pleuro-pedal connectives; *ped. g.* pedal ganglia; *pl. g.* pleural ganglion; *pl.-p. con.* pleuro-parietal connective; *r. visc. g.* right visceral ganglion; *r. br. n.* right branchial nerve; *r. buc. gang.* right buccal ganglion; *r. mant. n.* right mantle-nerve; *supra. g.* supra-intestinal parietal ganglion; *tent. n.* nerve to tentacle; *visc. com.* visceral commissure; *visc. n.* visceral nerve-branches.

right and left cerebral ganglia are fused together in the middle line, though separated by a constriction, and the ganglia of the two pairs are placed very close together, though quite distinct. From each cerebral ganglion there passes forwards a stout *cerebro-buccal connective* (*cer. buc. con.*) to a buccal ganglion (*r. buc. g.*) situated on the posterior surface of the buccal chamber. Also given off anteriorly from the cerebral ganglia are *optic nerves* (*opt. n.*) to the eye and tentacular nerves (*tent. n.*) to the tentacles. From each cerebral ganglion passes downwards and forwards a stout *cerebro-pedal connective*, and from each pleural ganglion a *pleuro-pedal connective*, to a large pair of closely-united *pedal ganglia* (Figs. 544 and 545, *ped. g.*) embedded in the upper layers of the muscles of the foot, to which they give off numerous nerves. The right pleural ganglion gives off behind a supra-intestinal *pleuro-parietal connective*, which bends across to the left, over the œsophagus, and some distance to the

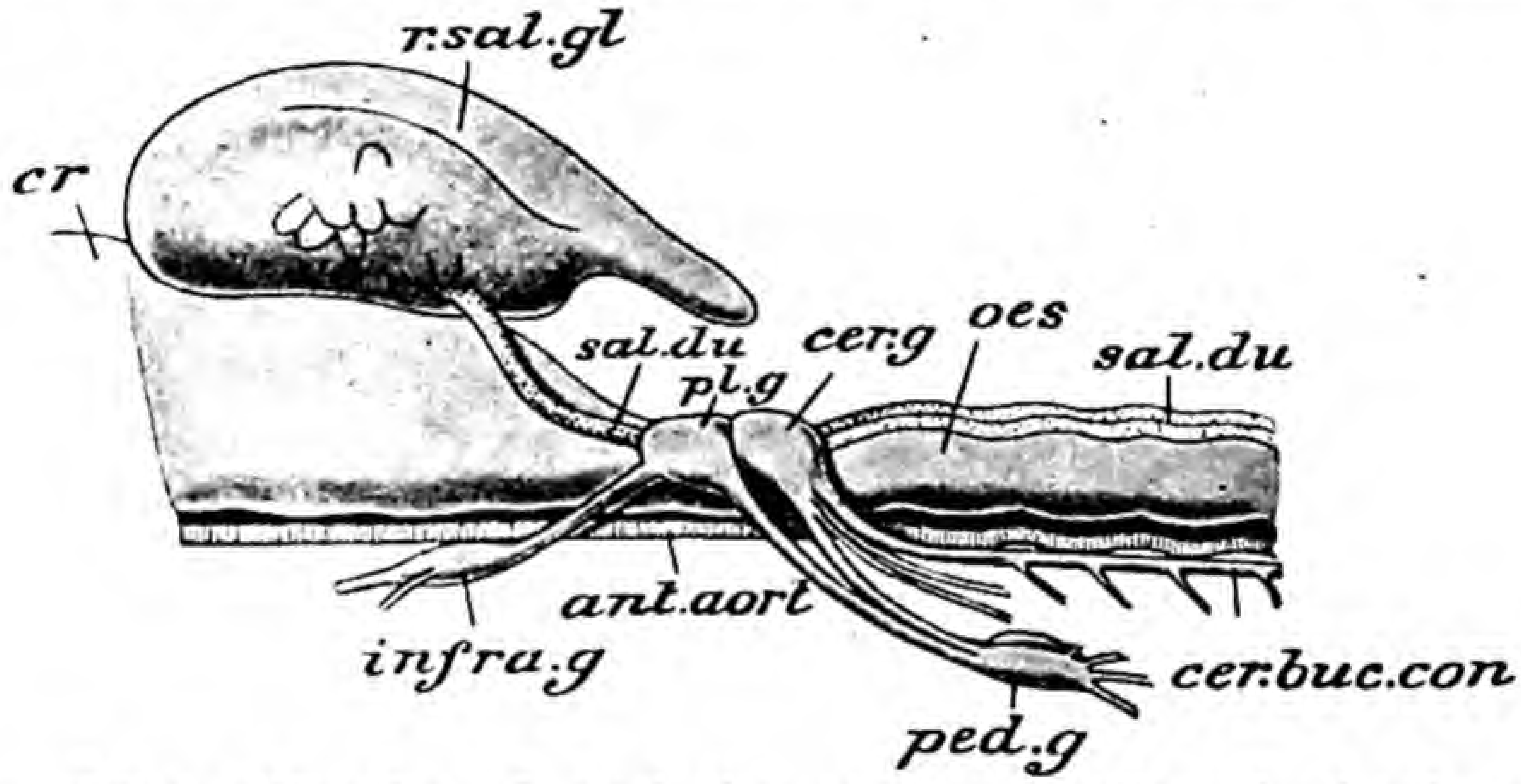


FIG. 545.—**Triton rubicundus.** Lateral view of nerve-ganglia and related parts. Letters as in Fig. 544; in addition—*ant. aort.* anterior aorta; *cr.* crop; *oes.* œsophagus; *sal. du.* salivary duct; *r. sal. gl.* right salivary gland.

left of the alimentary canal, expands into a triangular *supra-intestinal parietal ganglion* (*supra. g.*) situated below the superficial layer of muscular fibres. The left pleural ganglion gives off an infra-intestinal *pleuro-parietal connective*, which passes obliquely backwards and to the right, below the alimentary canal, to a ganglion situated a little to the right of the middle line—the *infra-intestinal parietal ganglion* (*infra. g.*). The supra-intestinal parietal ganglion gives off a nerve which runs towards the osphradium and ctenidium, which it supplies with nerve-branches, and units with a stout *mantle-nerve* (*l. mant. n.*), which is given off from the left pleural ganglion. The right pleural also gives off a stout connecting nerve to the infra-intestinal parietal ganglion. From the supra- and infra-intestinal parietal ganglia the left and right visceral connectives extend backwards and unite behind in the neighbourhood of the stomach; each ends in a triangular *visceral ganglion* (*l. visc. g.*; *r. visc. g.*), and these are joined by a transverse commissure (*visc. com.*), from which a number of visceral

nerves (*visc. n.*) are given off. The continuous strand of nervous tissue formed by the pleuro-parietal and the visceral connectives, together with the visceral commissure joining the two visceral ganglia, is usually called the visceral loop. A remarkable torsion of this visceral loop into the form of the figure "8" is here to be observed. This can be clearly seen from Fig. 544 by following the course of the visceral loop starting from the left pleural ganglion and proceeding along the pleuro-parietal connective to the infra-intestinal parietal ganglion and along the visceral connective to the right visceral ganglion; from there along the visceral commissure to the left visceral ganglion and along the visceral connective to the supra-intestinal parietal ganglion, and, following the pleuro-parietal connective, on to the right pleural ganglion, finally returning to the left pleural ganglion via the cerebral ganglia.

The **sense-organs** of Triton, in addition to the *tentacles* and the *osphradium*, which have been already referred to, are the *eyes* and the *statocysts*. The eye (Fig. 546) is a rounded invagination of the epidermis with an inner wall or *retina* (*ret.*) composed of pigmented and sensory cells. The outer wall is thin, and, with the overlying epidermis, forms a transparent *cornea*. In the interior of the eye is a clear rounded *lens* (*l.*) of dense cuticular matter secreted by the cells of the retina; this is surrounded by a less dense *vitreous* body.

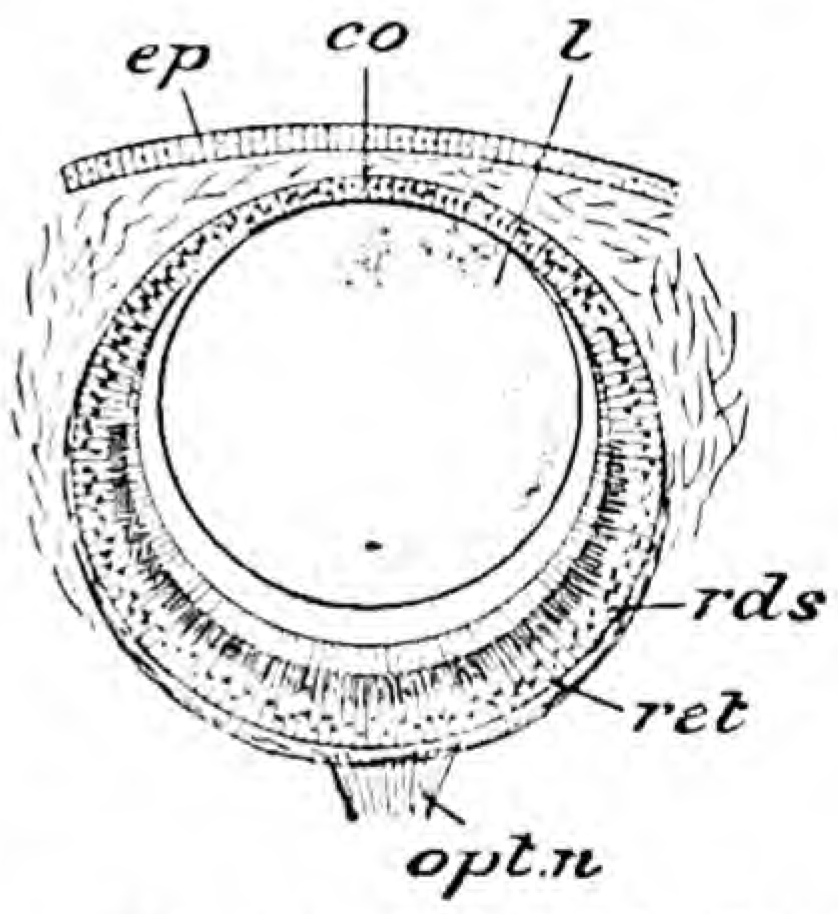


FIG. 546.—**Triton.** Section of the eye. *co.* cornea; *ep.* epidermis; *l.* lens; *opt. n.* optic nerve; *rds.* layer of rods (the line is not continued far enough inwards); *ret.* retina.

The **sexes** are distinct. There is a single gonad—*ovary* or *testis* as the case may be—lodged in the visceral spiral. The *sperm-duct* is a white tube, thickish and much convoluted where it leaves the testis, narrower and straight distally; it opens in front in the mantle-cavity into the proximal end of the sperm-groove, which, as already mentioned, runs forwards along the right side and becomes continuous with the groove traversing the penis. The oviduct (Fig. 541, *ovid.*) is proximally a very delicate tube with colourless, transparent walls. This runs forwards to the right side of the mantle-cavity, where it assumes the character of a stout tube (*ovid'.*) with thickened glandular walls, which passes forwards close to and parallel with the rectum, and opens on the exterior near the anus.

2. Distinctive Characters and Classification.

The Gastropoda are unsymmetrical Mollusca, with a mantle and a shell which consists of a single, unsymmetrical, usually spirally coiled valve, enclosing a visceral mass of corresponding form. There are, typically, two plume-like ctenidia

enclosed in a mantle-cavity, but there may be only one, or the ctenidia may be replaced by secondary gills ; and in air-breathing forms ctenidia are not developed, respiration taking place through the wall of the mantle-cavity itself. A distinct head bearing eyes and tentacles is present in the majority. The foot is situated behind the head, and usually has an extensive flattened ventral surface. The buccal cavity contains an odontophore with a radula bearing rows of chitinous teeth. The kidney is usually single. The nervous system contains distinct cerebral and pleural, besides buccal, pedal, parietal, and visceral ganglia. The sexes are sometimes separate, sometimes united. The larva passes through trochopore and veliger stages.

Class Gastropoda

ORDER 1.—PROSOBRANCHIA (STREPTONEURA).

Gastropoda in which, owing to torsion of the visceral hump, the visceral loop is in most cases twisted into a figure of " 8." The mantle-cavity opens anteriorly ; ctendia, if present, are situated in front of the heart ; the sexes are separate.

Sub-order a.—Aspidobranchia (Diotocardia).

Prosobranchia with the nervous system but little concentrated : the pedal ganglia are produced into long cords with the anterior ends of which the pleural ganglia are fused ; the cerebral ganglia wide apart ; the osphradium little developed. There is nearly always a single ctenidium or a pair ; ctenidia plume-like with two rows of leaflets, free distally. The ctenidia are sometimes missing, being then generally replaced by secondary gill-structures. The auricles and kidneys are usually paired.

Tribe 1.—Rhipidoglossa.

Aspidobranchia in which the radula is composed of rows of numerous narrow teeth ; ctenidia, auricles, and gills in many cases paired.

This group includes (*Fissurella, Haliotis* (*Ear-shell*), *Trochus, Turbo,* and others.

Tribe 2.—Docoglossa.

Aspidobranchia in which there is a radula with very few hooked teeth in each row ; there is either a single ctenidium or the ctenidium is replaced by secondary gills, or branchial structures are completely missing ; heart with one auricle.

This group includes *Acmæa, Patella* (*Limpet*) (Fig. 561) and others.

Sub-order b.—Pectinibranchia (Monotocardia).

Prosobranchia with a somewhat concentrated nervous system ; with a single well-differentiated pectinate osphradium ; only the topographically left ctenidium present ; ctenidium with one row of leaflets and with the stem

generally attached throughout its length to the wall of the mantle-cavity; heart with one auricle.

Tribe 1.—*Tænioglossa.*

Pectinibranchia in which the radula consists of rows, generally composed of seven teeth.

This group includes two sections: 1. the creeping *Platypoda* comprising *Solarium* (Fig. 548), *Paludina* and *Ampullaria* (both fresh-water forms), *Littorina* (Periwinkle), *Vermetus, Sigaretus* (Fig. 554), *Cypræa* (Fig. 550), *Triton* (Figs. 536, 539) and others. 2. the pelagic *Heteropoda* with *Atlanta* (Fig. 556), *Carinaria* (Fig. 552), and *Pterotrachea* (Fig. 557).

Tribe 2.—*Rachiglossa.*

Pectinibranchia in which the radula consists of rows with not more than three teeth. There is a highly developed proboscis, and always a pallial siphon.

This group includes *Buccinum* (Whelk), *Murex, Purpura, Nassa* and others.

Tribe 3.—*Toxoglossa.*

Pectinibranchia in which there are two large teeth in each row of the radula; œsophagus with poison gland.

This group includes *Terebra* (Fig. 549), *Conus* and others.

ORDER 2.—OPISTHOBRANCHIA (EUTHYNEURA I).

Marine Gastropoda with aquatic respiration, in which, owing to detorsion of the visceral hump, the widely open mantle-cavity shows a tendency to occupy a posterior position; the auricle of the heart is usually situated posterior to the ventricle; the ctenidium is often replaced by secondary branchiæ; the shell tends to be reduced, to become internal, or to be absent. The sexes are united.

Sub-order a.—Tectibranchia.

Opisthobranchia provided in nearly all cases with a mantle and a shell, nearly always with a true ctenidium, and an osphradium.

This group includes *Aplysia* (Sea-hare) (Fig. 555), the pelagic *Pteropoda* (Fig. 558) and others.

Sub-order b.—Nudibranchia.

Opisthobranchia which are devoid of a shell in the adult condition, and have no true ctenidia or osphradia; respiration carried on by means of secondary branchiæ usually arranged in a circlet around the anus, or in rows on the dorsal surface, or laterally under the edge of the mantle.

This group includes *Doris* (Fig. 551), *Pleurophyllidia* (Fig. 560), *Eolis, Tethys*, and other shell-less forms.

Order 3.—Pulmonata (Euthyneura II).

Hermaphrodite Gastropoda with two pairs of tentacles; without ctenidia; respiring through the wall of the mantle-cavity (*lung*), which has a narrow contractile aperture. Nervous system secondarily symmetrical, owing to shortening of connectives and concentration of ganglia into a circum-œsophageal ganglionic complex.

Sub-order a.—Basommatophora.

Pulmonata with eyes at the base of tentacles.

This group includes the fresh-water forms *Limnæa* and *Planorbis*, and a number of marine and brackish-water forms.

Sub-order b.—Stylommatophora.

Pulmonata with eyes at the tip of posterior pair of tentacles.

This group includes the Land-snails (*Helix*, Fig. 559) and the Slugs (*Limax*, Fig. 553).

3. General Organization.

External Features, Symmetry, etc.—Few Gastropods make an approach towards even superficial symmetry, and in cases in which there is a near approximation towards such a state of things, it seems clear, from the results of the study of development and of a comparison with allied forms, that the symmetry presented is not primitive, but has been secondarily acquired—such symmetrical forms having been derived from unsymmetrical ancestors.

The departure from symmetry is most marked in the majority of the Prosobranchia. It may be said to be due to the development of a protective shell composed of one piece and extensive enough to be capable of enclosing all the soft parts; and to the extension of the foot on the ventral side as an elongated muscular creeping organ. The development of the shell rendered necessary an arrangement of the parts whereby the mantle-cavity with the anus, the ctenidia, and the excretory apertures should come to be situated towards the head-end of the animal. The mantle-cavity and associated parts (*pallial complex*, as the whole is termed) had, therefore, to be shifted forward from its primitive posterior position, and this was probably effected by arrest or retardation of growth on one side and active extension on the other. In the majority of cases it is the right side the growth of which becomes retarded, and, in consequence, it is on the right side that the pallial complex comes to travel forwards. The effect is as if, the head retaining its symmetry, the parts between it and the anus had undergone a process of rotation or *torsion* through about 180° around a vertical axis passing in a dorso-ventral direction—the direction of torsion being anti-clockwise (Fig. 547).

With regard to the spiral form assumed by the shell in all highly developed Gastropods, it can only be pointed out here that, given the necessity for complete protection, compactness, and a provision for continuous growth, the spirally-coiled cone is the form of shell best adapted to all the conditions

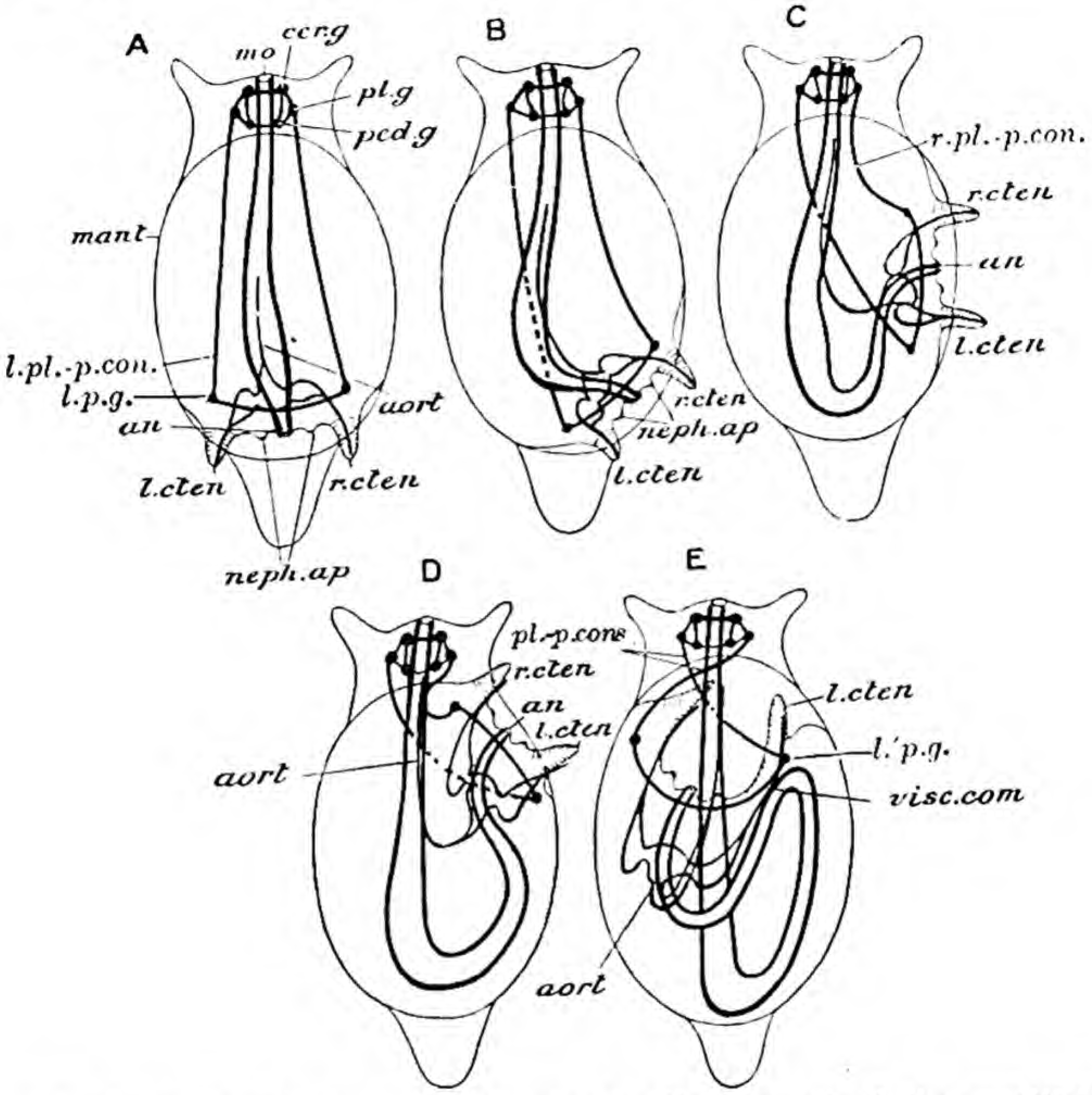


FIG. 547.—Diagrammatic representation of the displacement of the mantle-cavity and associated parts in the **Gastropoda.** Enteric canal blue, blood-system red. *A* represents a nearly symmetrical arrangement; in *B, C, D* are represented successive stages of displacement of the mantle-cavity to the right and forwards; in *E* the anus and (primarily) right ctenidium have passed the middle line. *an.* anus; *aort.* aorta; *cer. g.* cerebral ganglion; *l. cten.* left ctenidium; *l. p. g.* left parietal ganglion; *l'. p. g.* primitively left, now topographically right parietal ganglion (infra-intestinal parietal ganglion); *l. pl.-p. con.* left pleuro-parietal connective; *mant.* mantle; *mo.* mouth; *neph. ap.* renal apertures; *ped. g.* pedal ganglion; *pl. g.* pleural ganglion; *pl.-p. cons.* pleuro-parietal connectives; *r. cten.* right ctenidium; *r. pl.-p. con.* right pleuro-parietal connective. (After Korschelt and Heider.)

A straight cone, however directed, would be a great impediment to active progression, and the coiling in a compact spiral would seem to be the line of development best adapted to secure concentration and strength.

The shifting of the pallial complex in many Streptoneura proceeds so far that the complex completely or partially passes across the middle line, and the

anus comes to be situated to the left of the mouth. The displacement of the pallial complex involves two important series of changes in the internal organs, in addition to the suppression of certain structures to be referred to presently. In the first place there is necessarily involved a throwing of the enteric canal into a loop (Fig. 547), and in the second place the long pleuro-parietal connectives become twisted in such a way as to assume the form of the figure 8—the right connective becoming *supra-intestinal* and the left *infra-intestinal.*

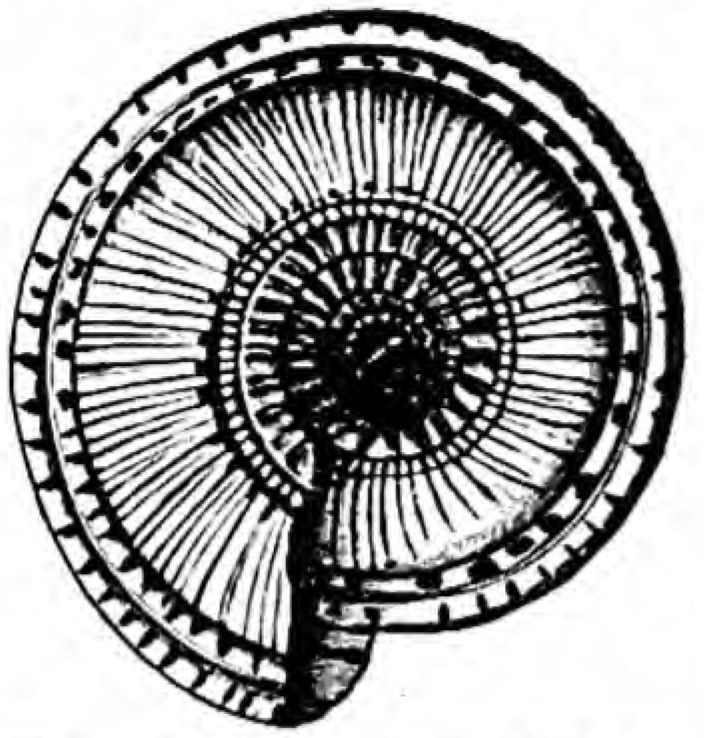


FIG. 548.—Shell of **Solarium perspectivum,** from the under side. (From the *Cambridge Natural History.*)

Universally accompanying the process of forward displacement of the pallial complex, except in *Haliotis* and *Fissurella* and allied Rhipidoglossa, occurs the reduction of its paired parts. Thus in all the more highly developed Prosobranchia the primitively right (topographically left) ctenidium alone persists, and one of the two kidneys is alone fully developed and functional.

In the Opisthobranchia there are distinguishable various stages in a process of *detorsion* by which the torsion tends to be reversed and the pallial complex carried back towards the posterior end along the right side. The visceral loop loses its twisted arrangement in nearly all such cases; but there is the same reduction of the paired parts of the pallial complex as in the Prosobranchia.

FIG. 549.—Shell of **Terebra oculata.**

The **shell** in the adult Limpets (*Patella* and allied genera) has the form of a short cone. In most of the Gastropoda it has the shape of a spiral with the turns usually in close contact with one another, the inner walls of the turns coalescing to form an axial, hollow or solid column—the *columella*. The portion of the shell projecting inwards between the turns of the spiral sometimes becomes absorbed. In certain cases, on the other hand, the cavity of the apical portion of the spiral may be cut off from the cavity of the rest of the shell by the formation of a transverse partition, the animal then becoming restricted to the basal portion; or several such partitions may be formed. By far the greater number of such spiral shells are *dextral, i.e.,* if we begin at the apex of the spiral to reach the opening of the shell we have to pass from left to right, with the columella always on our right-hand side: in a few cases, however, the spiral is *sinistral,* taking the opposite direction from that of the ordinary dextral

shell. The form of the shell varies with the degree of obliquity with which the whorls are set on the axis. When the obliquity is very slight (Fig. 548), the spiral is nearly flat; when the obliquity is great, an elongated tapering shell such as that represented in Fig. 549 is the result. Sometimes the later whorls completely cover over the earlier ones, so that the spiral form of the shell is concealed. Sometimes only the apical portion of the shell is spiral, the remainder being a straight or sinuous cylinder. The spiral form of the shell and the parts enclosed in it, as well as the direction of the spiral, whether dextral or sinistral, are, it may be here pointed out, very fundamental features of the organization of the Gastropod, and are foreshadowed at an early stage in the cleavage of the ovum. The mouth of the shell has usually a prominent margin or *peristome*, which is sometimes entire and continuous, sometimes broken by a deep notch or a spout-like process or canal, formed in connection with the development of a spout-like prolongation of the mantle, the *siphon*, which lies in it. The mouth of the shell in many Gastropoda is capable of being

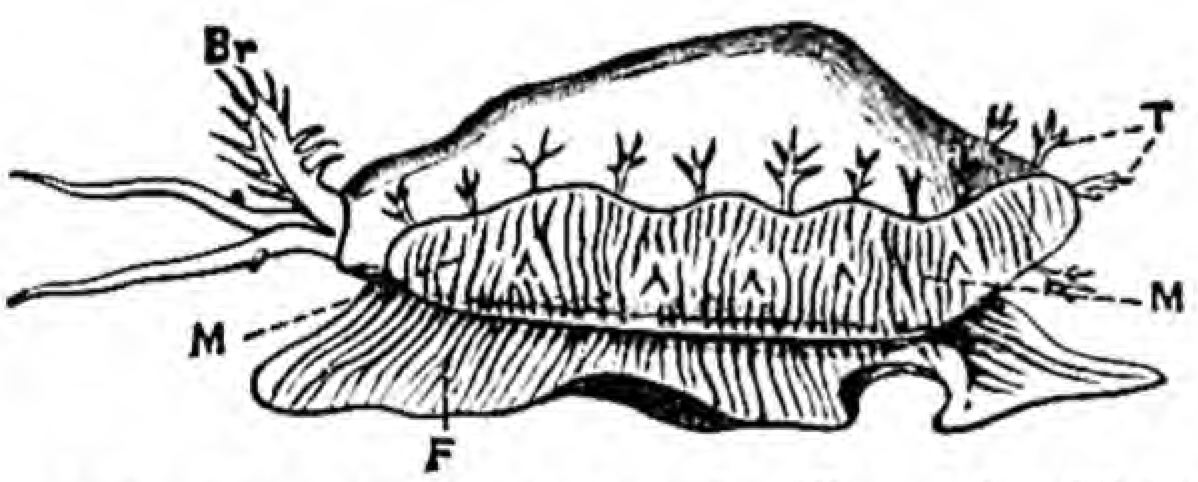


FIG. 550.—**Cypræa moneta** (Cowrie). Showing the mantle, provided with marginal tentacles, partly enveloping the shell. *Br.* siphon; *M. M.* mantle; *F.* foot; *T.* tentacles at the edge of the mantle. (From Cooke, after Quoy and Gaimard.)

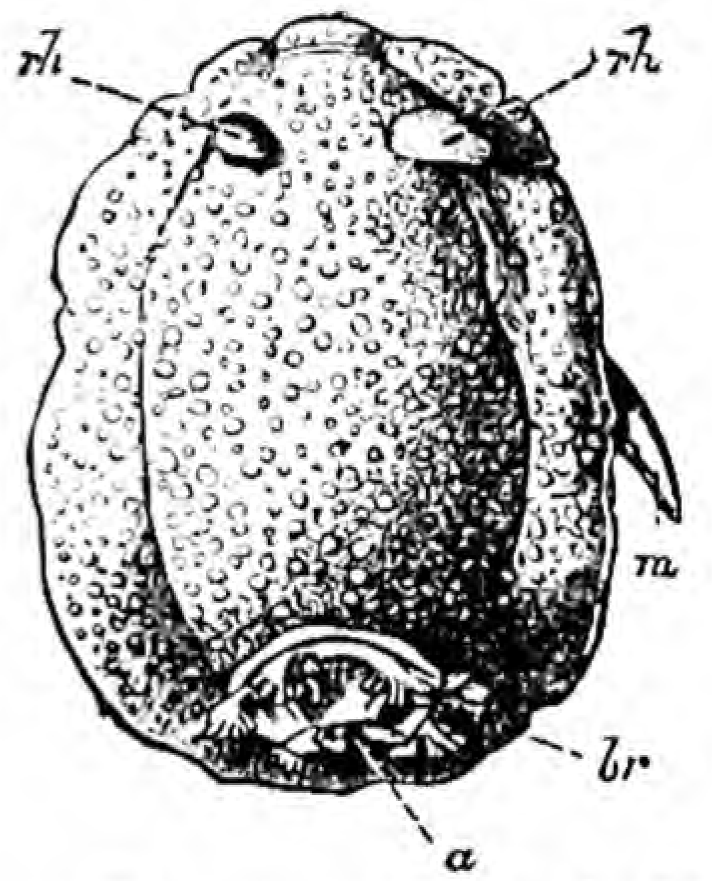


FIG. 551.—**Doris (Archidoris) tuberculata.** *a.* anus; *br.* branchiæ; *m,* penis; *rh, rh,* tentacles. (From the *Cambridge Natural History*.)

closed by means of an *operculum* borne on the foot. In some terrestrial forms in which an operculum is absent, the opening may be closed up during winter by a layer of hardened mucous matter to which the name of *epiphragm* is applied. The margin of the mantle in some cases bears a series of *tentacles*. Lateral folds of the mantle are in some of the Gastropoda (Fig. 550) reflected over the shell and may completely cover it. In some cases these folds unite by their edge, so that the shell comes to be enclosed in a complete sac of the mantle; such enclosed shells are always imperfectly developed and incapable of covering the body. Thus in *Aplysia* (Fig. 555) and some other Opisthobranchs the shell is greatly reduced, thin and horn-like, and concealed within the mantle, while in the nudibranch members of the same order it is entirely absent (Fig. 551). The shell is also completely absent in some of the pelagic forms (*Heteropoda and Pteropoda*); in others, though present and external, it is too small to enclose the animal (Fig. 552). In the Slugs, among the Pul-

monata, the shell is vestigial and in most cases is concealed by the mantle (Fig. 553).

The **foot** varies in the extent of its development in the different families of the class. It usually presents an elongated flat ventral surface on which the animal creeps by wave-like contractions of the muscular tissue. An

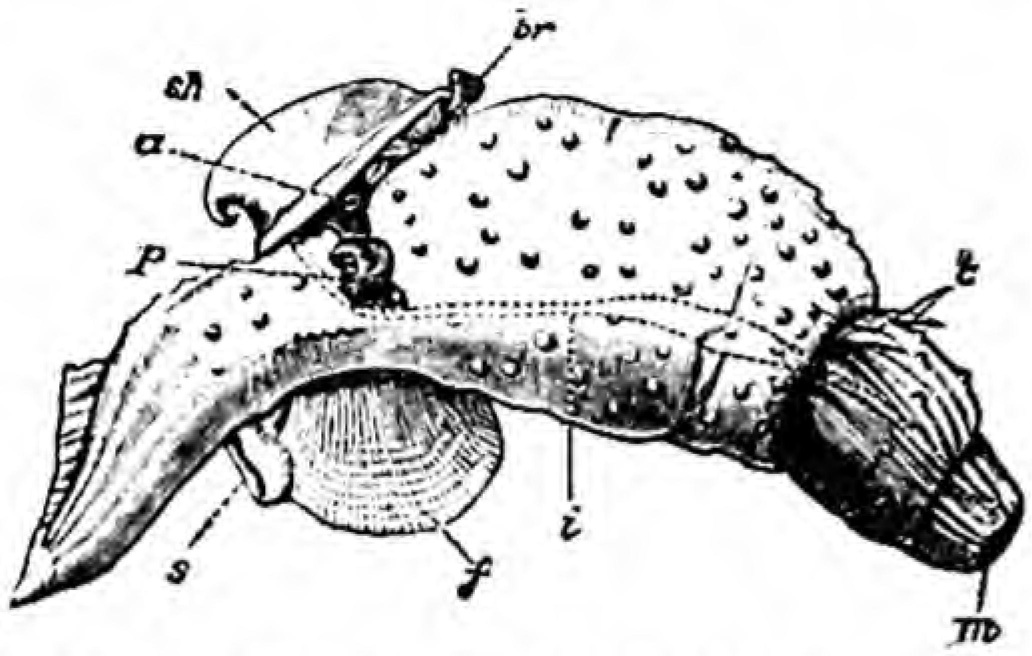


FIG. 552.—**Carinaria mediterranea.** *a.* anus; *br.* branchia; *f.* foot; *i.* intestine; *m.* mouth; *p.* penis; *s.* sucker; *sh.* shell; *t.* tentacles. (From the *Cambridge Natural History.*)

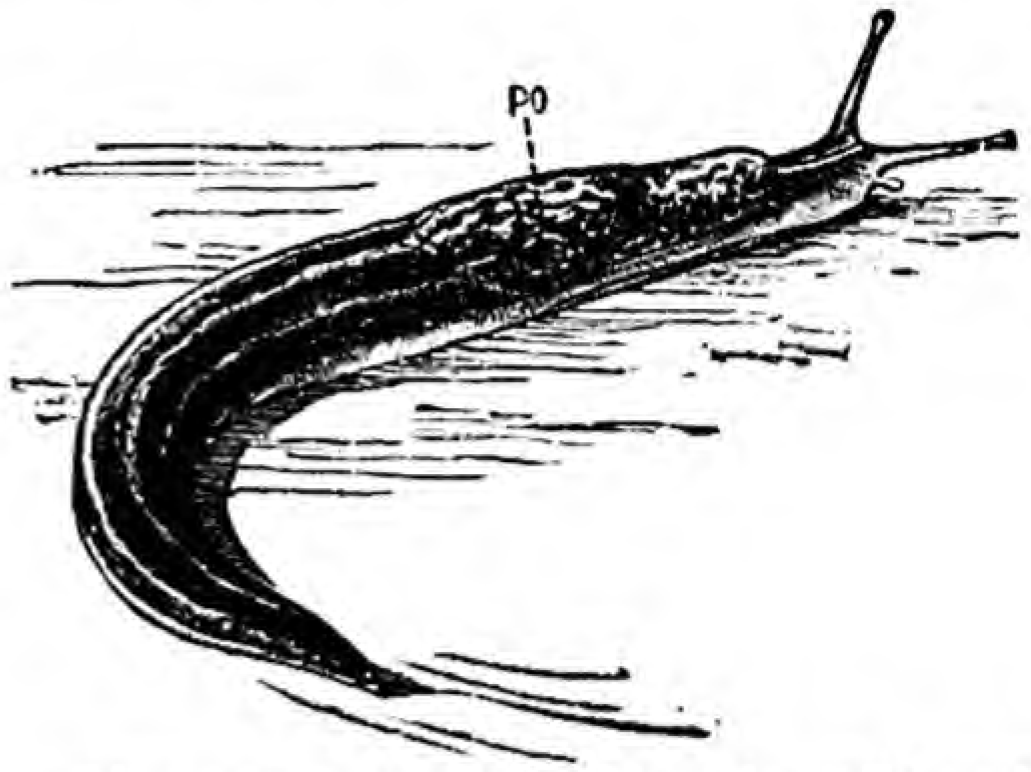


FIG. 553.—A Slug (**Limax**). *PO*, pulmonary aperture. (From the *Cambridge Natural History.*)

exceptional case is that of Cæcum, in which the creeping movement is supposed to be entirely due to the action of cilia covering the ventral surface. In the typical Gastropods the foot is usually distinguishable into three parts, a middle part or *mesopodium*, which is the most important, with a smaller anterior *propodium* and posterior *metapodium*. In many burrowing forms (Fig. 554)

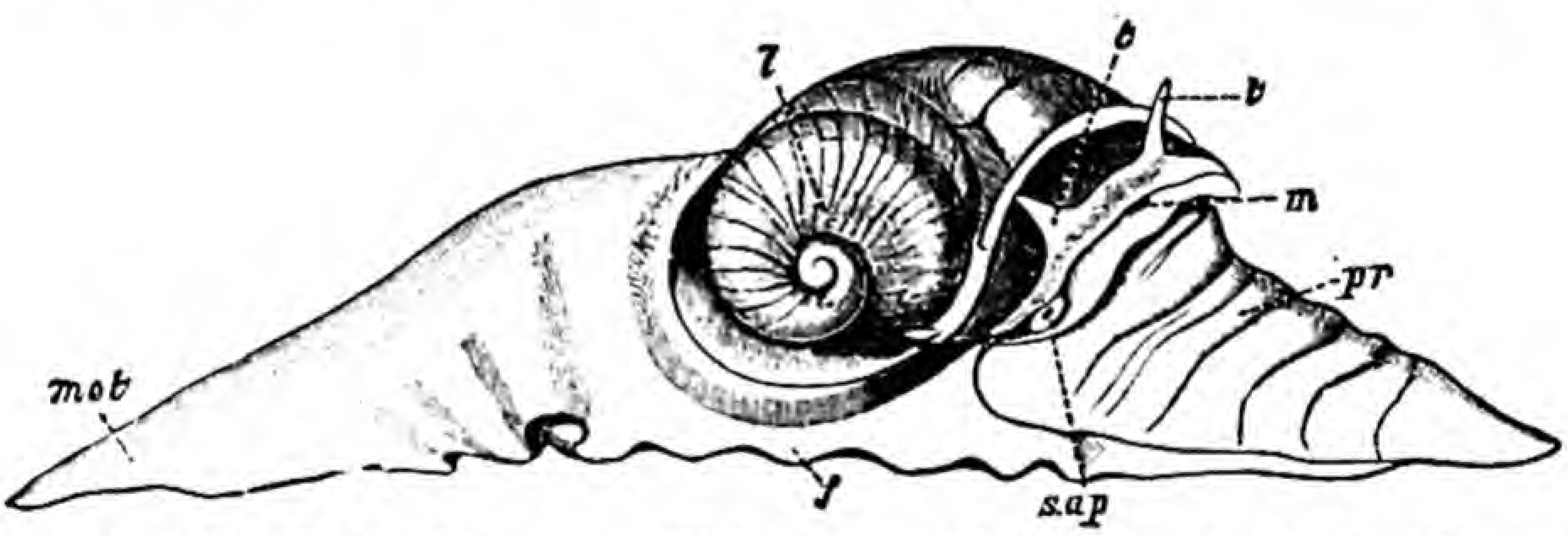


FIG. 554.—**Sigaretus lævigatus,** exemplifying great development of propodium (*pr.*) and metapodium (*met.*), in a burrowing Gastropod. The shell has been removed. *f.* mesopodium; *l.* " liver "; *s. ap.* aperture of siphon; *t. t.* tentacles. (From the *Cambridge Natural History,* after Quoy and Gaimard.)

the propodium is well developed and sharply marked off to act as a burrowing organ. In a few cases a pair of tentacles—the *pedal tentacles*—are situated at the anterior end of the foot; still rarer is a pair of similar appendages at the posterior end. The whole foot becomes reduced in the few Gastropods that remain fixed. The metapodium very usually in the Prosobranchia bears a disc or stopper—the *operculum* already referred to—usually horn-like, rarely completely calcified, more commonly horn-like with a thin calcareous invest-

ment—by means of which the aperture of the shell is closed when the animal is retracted.

In some forms, such as the Sea-hares (*Aplysia*, Fig. 555), the foot develops a pair of lateral lobes—the *parapodia*—which act as fins; and in the Pteropods (Fig. 558), which are specially modified for a pelagic existence, these constitute the largest part of the foot. In the Heteropoda (Figs. 552, 556, 557), which are also pelagic, the foot is also modified to act as a swimming organ. In one family of this group (Fig. 556) all three parts of the foot are well developed, the mesopodium bears a sucker, and the metapodium an operculum (*p.*); in the rest the mesopodium is alone well developed and forms a laterally-compressed, vertically-elongated fin. The term *epipodium* is applied to a ridge or fold, which, when best developed, runs around the entire side of the foot, and may be beset with papillæ or tentacle-like processes.

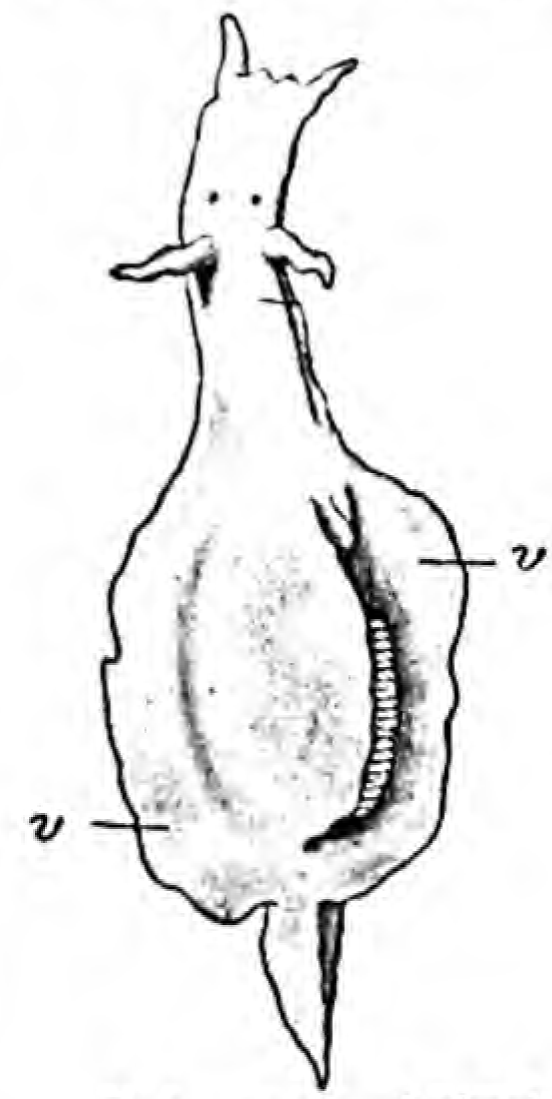


FIG. 555.—**Aplysia,** dorsal view. *v*, parapodia. (After Keferstein.)

A *pedal gland* is present in the majority: it is a simple or branched invagination of the integument, lined by mucus-secreting cells. Very commonly, as in Triton, it opens on the exterior in the middle line of the ventral surface of the foot.

The Gastropoda have a well-marked **head,** separated from the body by a

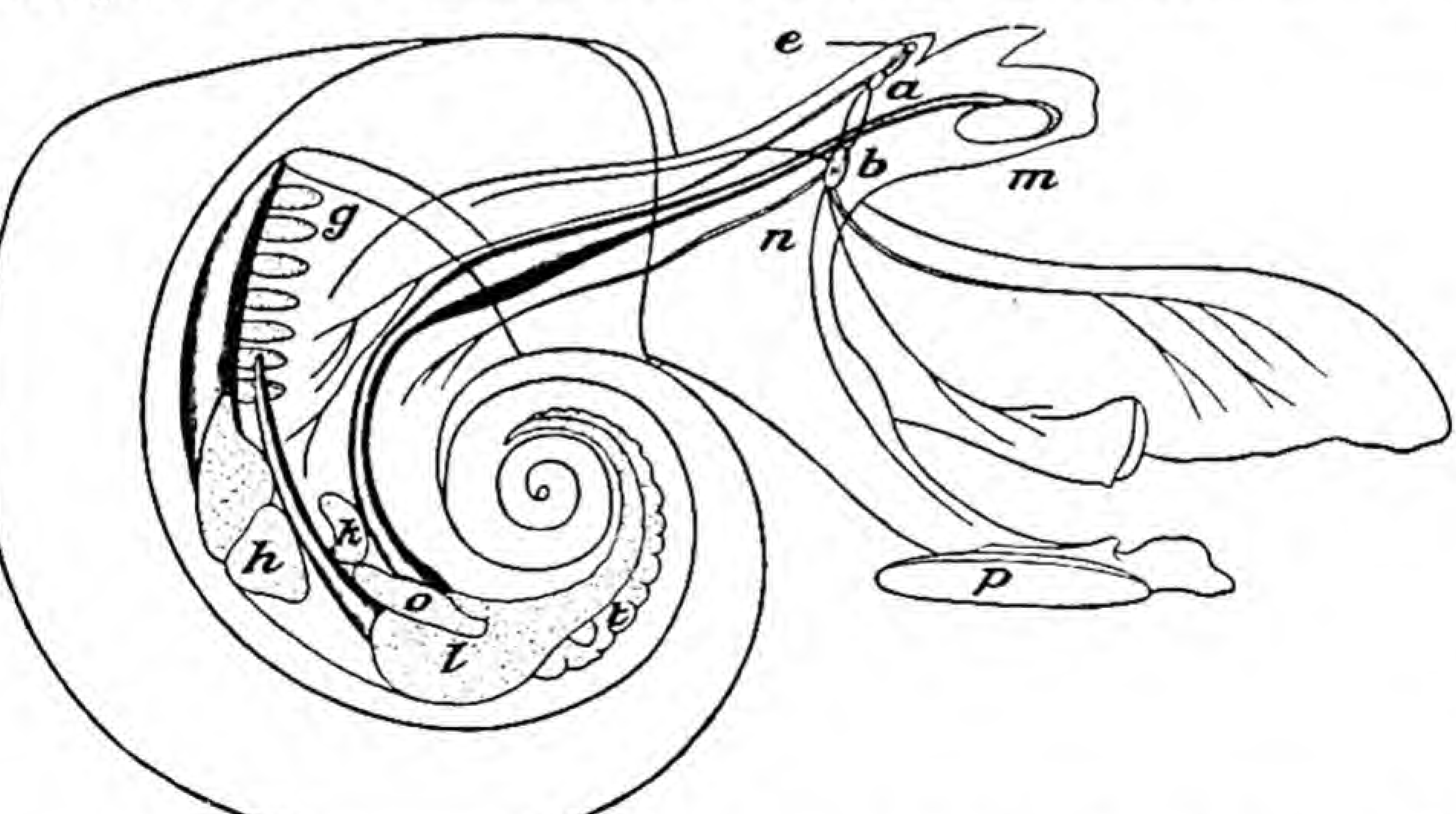


FIG. 556.—**Atlanta peronii.** *a.* cerebral ganglia; *b.* pedal ganglia; *e.* eye; *g.* ctenidia; *h.* heart; *k.* kidney; *l.* "liver"; *m.* mouth; *o.* ovary; *p.* operculum; *t.* testis.

constriction or *neck.* The mouth, situated at the anterior end of the head on its ventral aspect, is in many instances provided with a protrusible proboscis or *introvert,* sometimes of considerable length. In the dorsal surface of the

head are a pair of tentacles which vary a good deal in shape, but are usually cylindrical or club-shaped. In most cases the eyes are situated on tubercles at the bases of the tentacles, or elevated towards the middle; but in the Snails

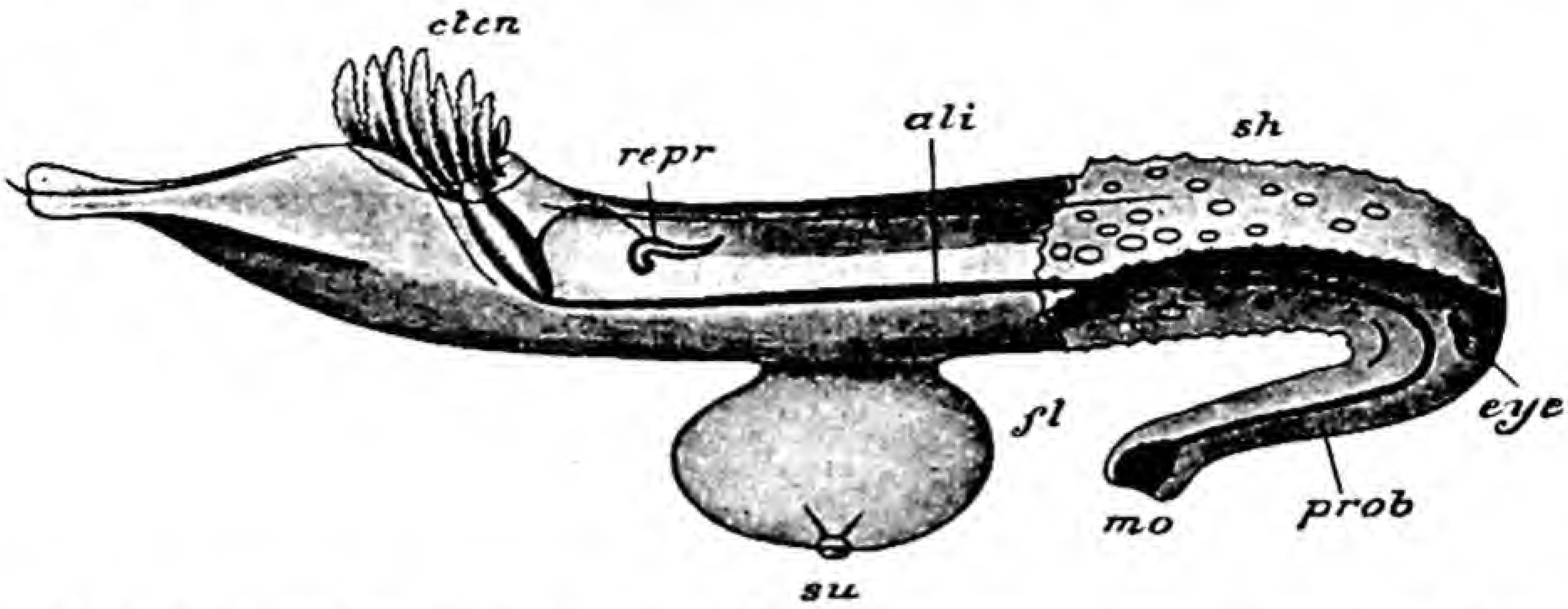


FIG. 557.—**Pterotrachea scutata.** *ali.* alimentary canal; *cten.* gills; *eye,* eye; *fl.* float; *mo.* mouth; *prob.* proboscis; *repr.* gonad; *sh.* shield covering a portion of the dorsal surface; *su.* sucker.

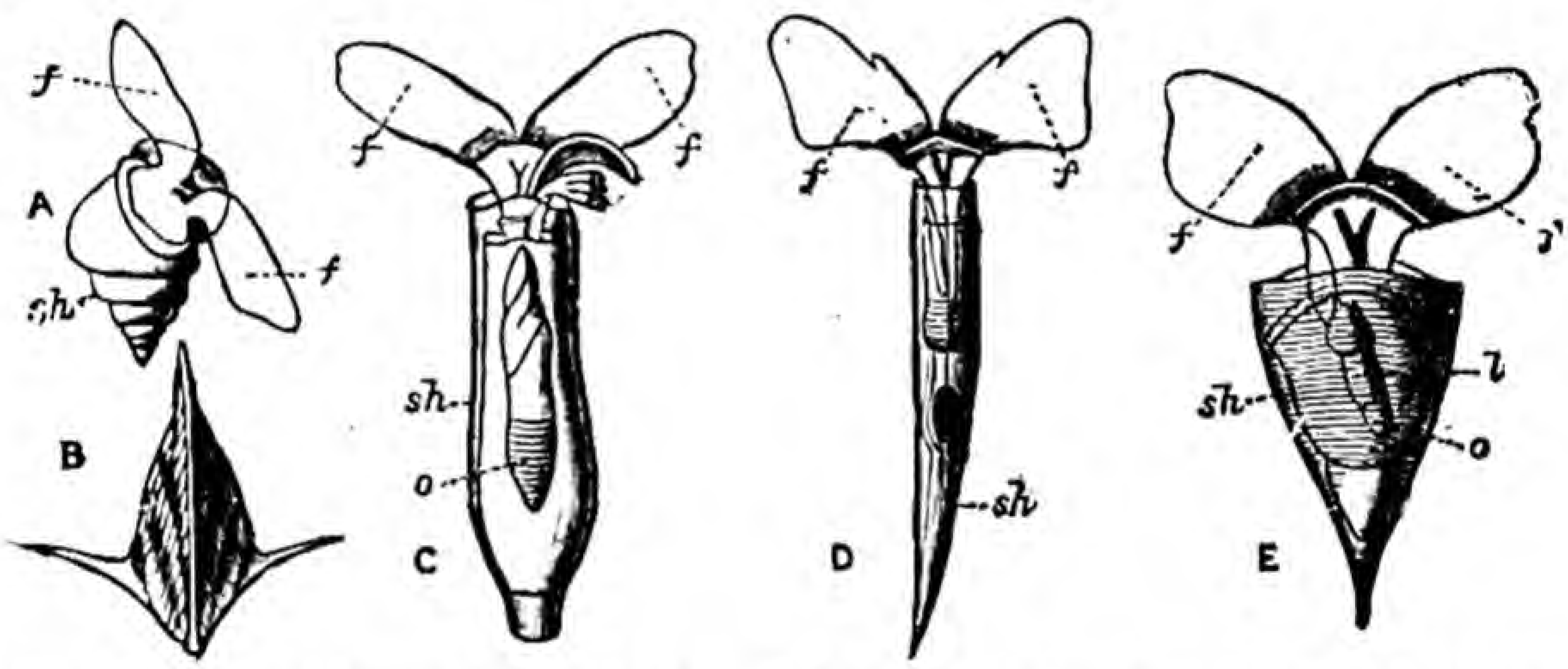


FIG. 558.—Shell-bearing **Pteropoda.** *f. f.* fins; *l.* "liver"; *o.* ovary; *sh.* shell. (From Cooke, after Souleyet.)

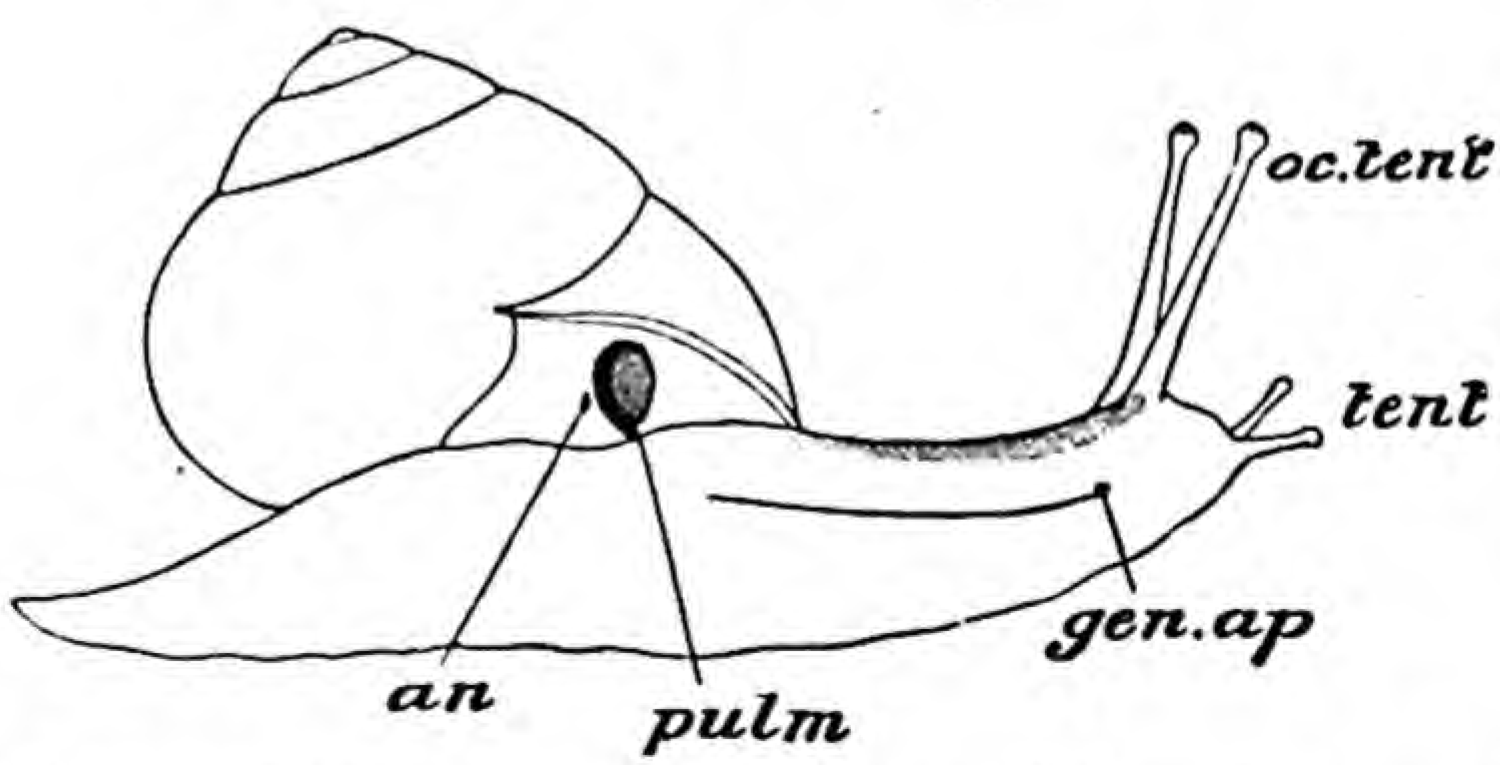


FIG. 559.—**Helix nemoralis.** *an.* anus; *gen. ap.* genital aperture; *oc. tent.* posterior eye-bearing tentacles; *pulm.* opening of pulmonary sac; *tent.* anterior tentacles. (After Pelseneer.)

and Slugs (Fig. 559) the eyes are elevated on the extremities of a second, longer, pair of tentacles (*oc. tent.*) placed behind the first.

The **mantle** is usually developed into a fold—the *mantle-flap*—originally

posterior, but subsequently becoming shifted round, in the course of the displacement already referred to, to the right-hand side. This covers over a cavity—the *mantle-cavity*—situated anteriorly, in which are situated the anal and renal apertures and the ctenidia. The edges of the mantle-flap may become united together in such a way as to form a chamber opening on the exterior by a comparatively narrow opening. In many of the Prosobranchia the edges of this aperture are drawn out into a spout-like prolongation open ventrally —the *siphon*—which lies in the corresponding prolongation of the peristome of the shell and serves as a channel for the ingress and egress of water. In

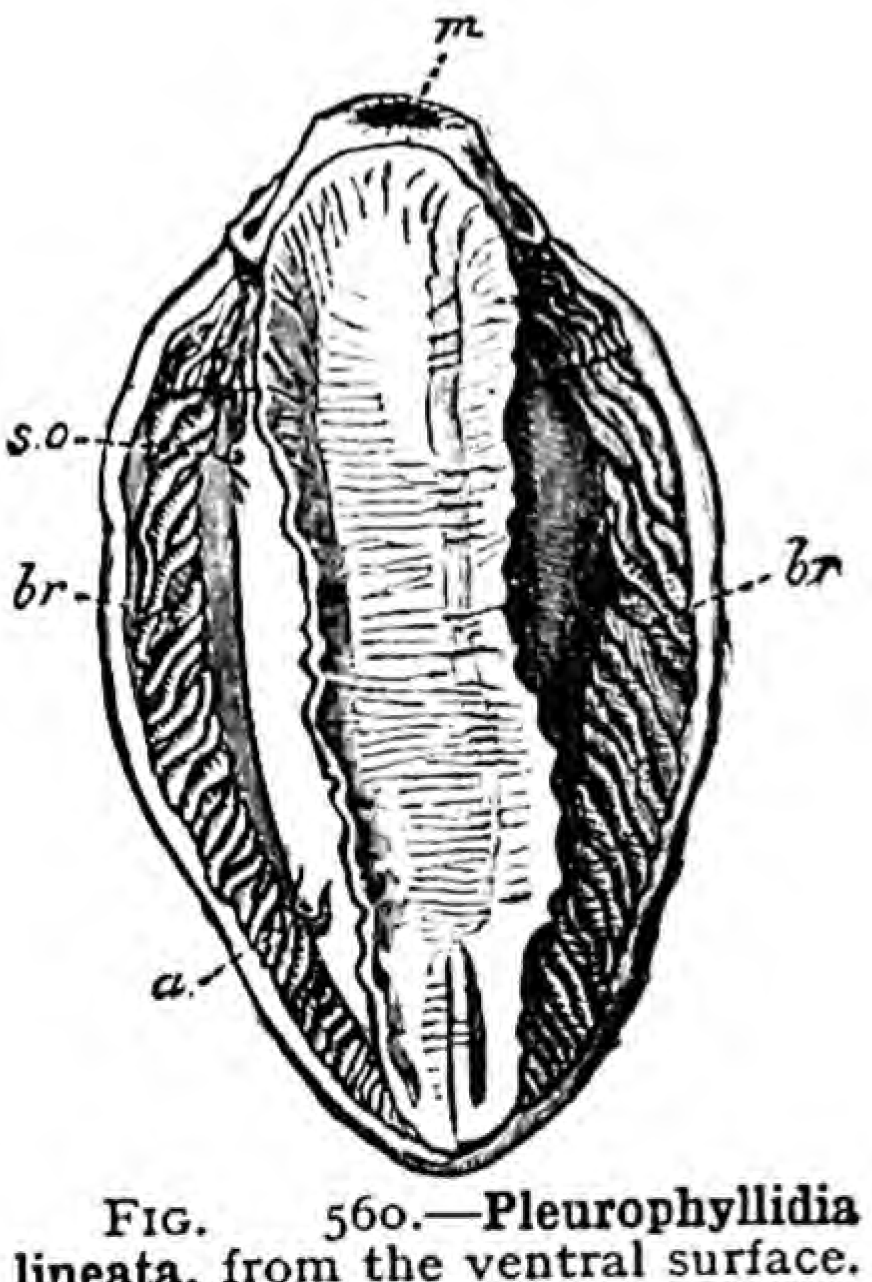


FIG. 560.—**Pleurophyllidia lineata,** from the ventral surface. *a.* anus; *br.* secondary branchiæ; *m.* mouth; *s. o.* sexual opening. (From the *Cambridge Natural History.*)

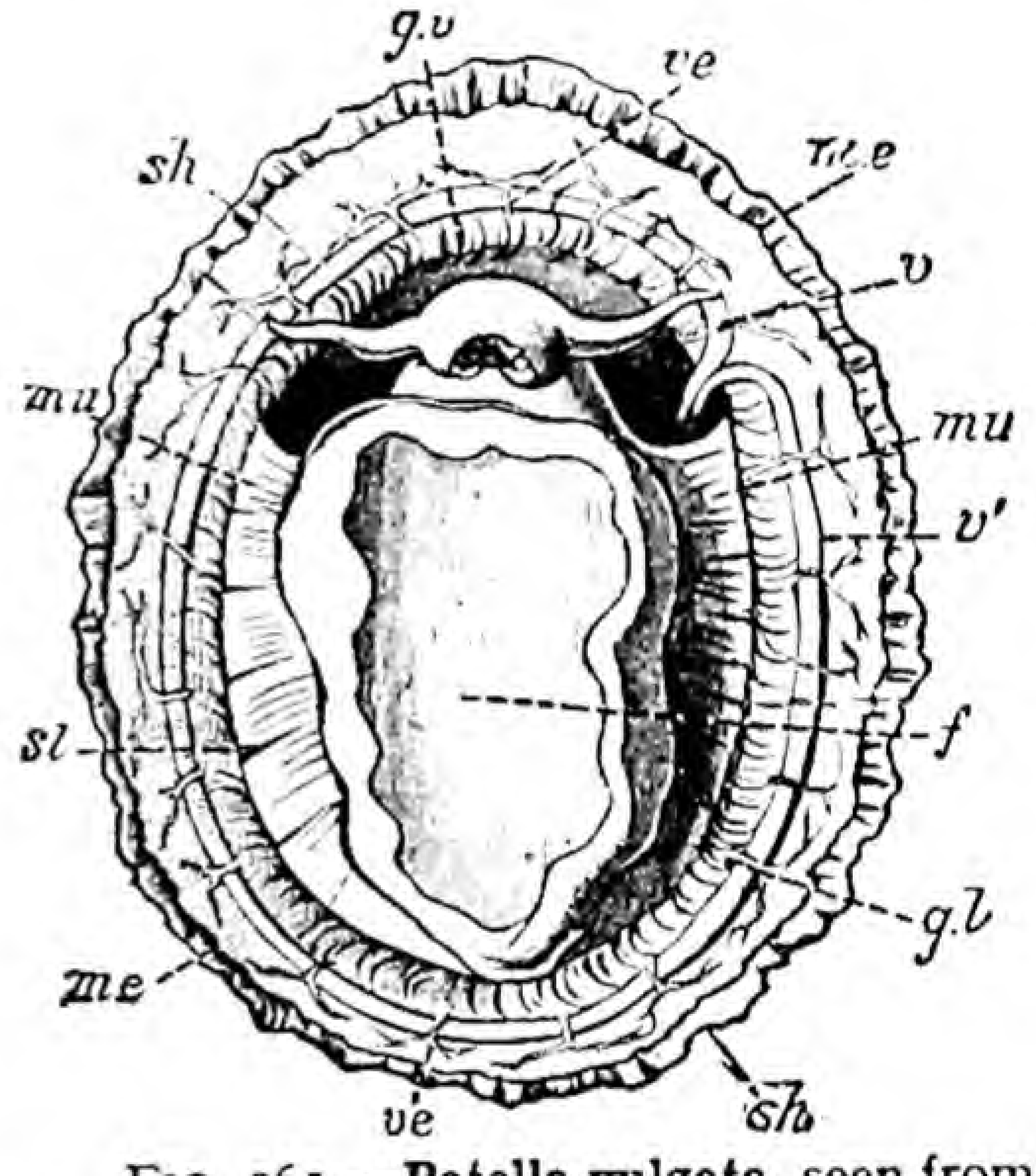


FIG. 561.—**Patella vulgata,** seen from the ventral side. *f.* foot; *g. l.* circlet of gill-lamellæ; *m. e.* edge of the mantle; *mu.* attachment-muscle; *sl.* slits in the attachment-muscle; *sh.* shell; *v.* efferent branchial vessel; *v'.* aorta; *ve.* smaller vessels. (From the *Cambridge Natural History.*)

some Gastropods, however, there is no definite mantle-cavity, the anus, renal apertures, and ctenidia merely lying under cover of a comparatively slightly developed lateral mantle-flap. Usually there is on the inner surface of the mantle a glandular area—the *pallial mucus-gland.*

Respiratory Organs.—There are typically two ctenidia, one on the right side and the other on the left, contained in the mantle-cavity; but in the great majority of the Prosobranchia and branchiate Opisthobranchia the primitively right (topographically left) ctenidium alone is retained. In those Gastropoda that possess two ctenidia, and in many forms with only one, the axis of the ctenidium bears two rows of compressed filaments, and is attached only towards its base. But in the majority of those with one ctenidium there is, as in

Triton, only a single row of filaments retained, and the organ is attached throughout its length.

In the Limpets (Patella and its allies, Fig. 561) the true ctenidia are represented only by a pair of vestiges, and respiration is carried on by a number of secondary branchiæ (*g. l.*) in the form of lamellæ situated between the short lateral fold of the mantle and the foot.

In the Nudibranchs true ctenidia are absent, but their place as breathing organs is taken by a number of *secondary branchiæ*, sometimes simple, sometimes branched or pinnate processes, which are distributed over the dorsal surface, as in *Eolis*; or, as in *Doris* (Fig. 551), form a circlet surrounding the anus; or, as in *Pleurophyllidia* (Fig. 560), a row on each side beneath the mantle-flap.

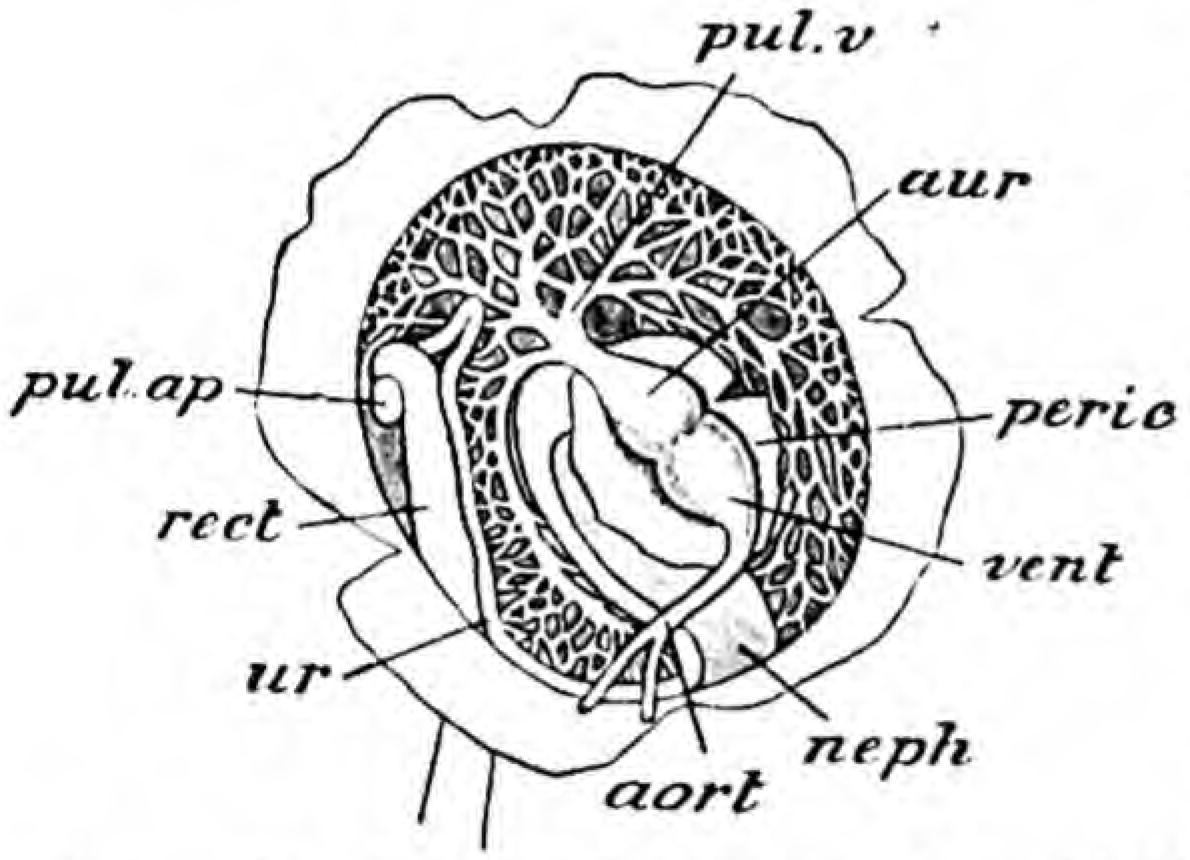


FIG. 562.—Pulmonary cavity and related parts in a Slug (**Limax**). *aort.* aorta; *aur.* auricle; *neph.* kidney; *peric.* pericardium, laid open; *pul. ap.* pulmonary aperture; *pul. v.* pulmonary vein with its ramifications; *rect.* rectum; *ur.* ureter; *vent.* ventricle. (After Pelseneer.)

In the *Pulmonata*, and in some members of other groups, ctenidia are absent, and the mantle-cavity, completely enclosed except for a small rounded opening, has the function of a **pulmonary sac** or **lung** (Fig. 562), its roof being richly supplied with blood-vessels. In one family of Pulmonata, the pulmonary chamber gives off a number of branching air-tubes or *tracheæ*. In some of the Pulmonata there is a return to a completely aquatic mode of respiration accompanied by the development of *secondary gills*—vascular processes of the wall of the mantle-cavity.

Near the base of each ctenidium is an elevation—the **osphradium**—corresponding to the body of that name in other Mollusca and having a similar function.

Digestive Organs.—In many Prosobranchia there is a long *introvert*, capable of being everted and retracted, at the extremity of which the mouth is placed. A single curved horny jaw lies on the roof of the buccal cavity in the Pulmonata; in most Prosobranchia (as in Triton) the place of this is taken by two lateral pieces.

A characteristic feature of the alimentary canal is the possession of an odontophore and radula, a typical example of which has been described in that of Triton. In the different groups differences are observable in the radula as regards the proportions of the parts, and the size, form, and arrangement of the teeth. As shown in the classification, these differences are of great

systematic importance. A few of the most important types of radula are represented in Fig. 563. The structure and relations of the alimentary canal are similar to those already described in Triton, and salivary glands and "liver" (hepato-pancreas) are always present.

In some Opisthobranchia the stomach contains a series of teeth which are sometimes sharp and chitinous, sometimes plate-like and calcified. Frequently a special development of the cuticular lining of the stomach forms a hard rod —the *crystalline style*, lodged in a cæcum and comparable to the body of the same name in the Bivalvia (*vide infra*, p. 603). A pyloric cæcum is frequently appended to the stomach. The intestine is long and thrown into folds in the vegetable-feeding forms, short and straight in the carnivorous. In some

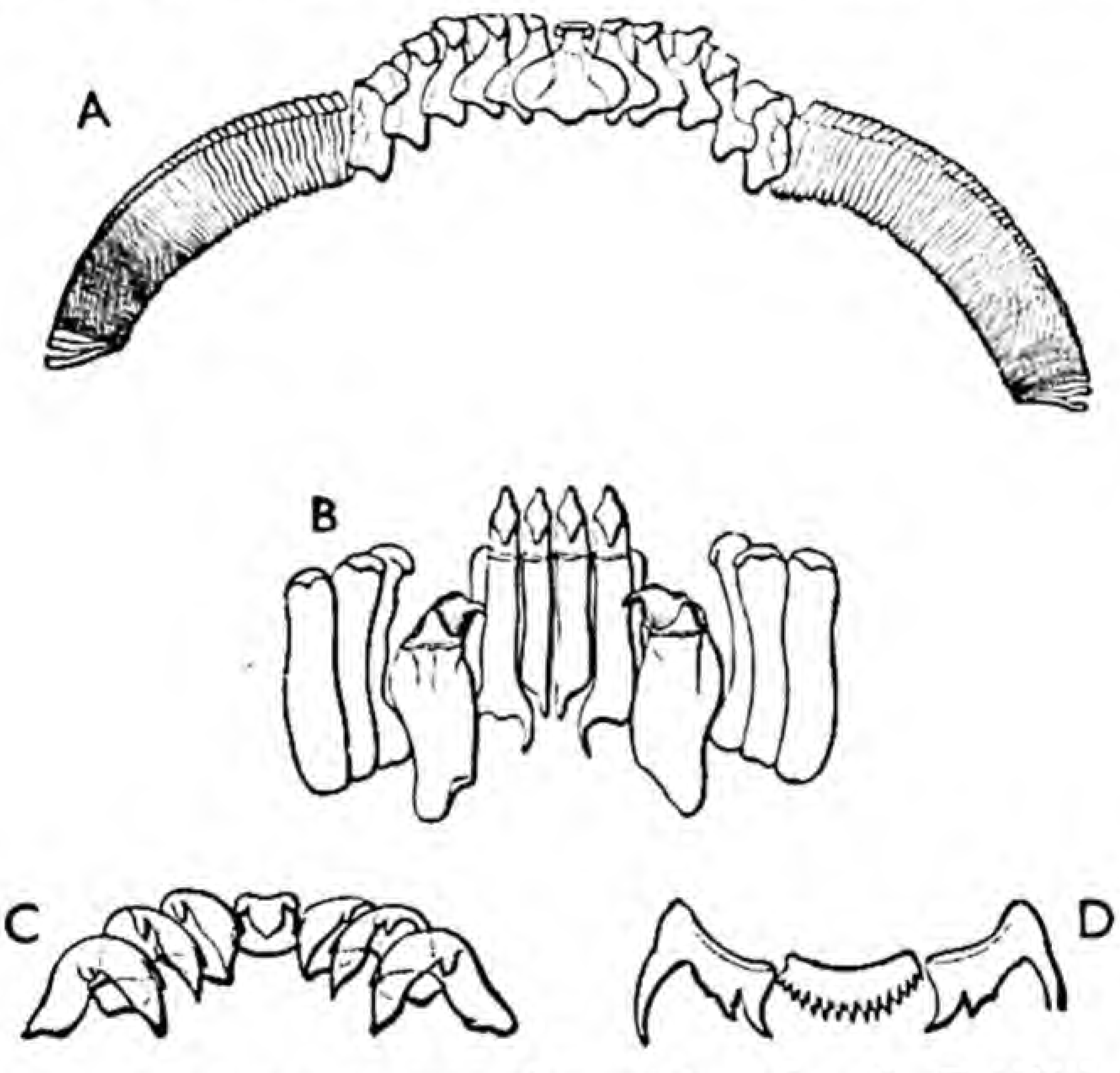


FIG. 563.—**Types of rows of teeth** from the radulæ of: *A*, *Trochus* (rhipidoglossate); *B*, *Patella* (docoglossate); *C*, *Cypræa* (tænioglossate); *D*, *Nassa* (rachiglossate). (From Lankester's *A Treatise on Zoology* (Adam & Charles Black), after Pelseneer.)

cases, *e.g.*, *Haliotis*, it traverses the ventricle, in others the pericardium; in others it passes through the kidney. In *Eolis* (Nudibranchia) the stomach gives off a number of glandular cæca which penetrate into the interior of the secondary branchiæ or *cerata* on the dorsal surface; these cæca take the place of the "liver" of other Gastropoda. In some of the Pectinibranchia there is a peculiar *adrectal gland*, situated at the side of the rectum and secreting a colourless fluid, which in *Murex* and *Purpura* turns purple on exposure to the air, and was anciently used as a dye—the "Tyrian purple."

The **heart** is, as in other Molluscs, enclosed in a special cavity—the *pericardium*—a specialized part of the cœlome, communicating with the cavity of the kidneys. It consists usually, as in Triton, of two chambers—auricle and ventricle; but in some, the Aspidobranchia, there are two auricles and a

ventricle. In the Opisthobranchia, as already mentioned, it lies in front of the ctenidia; in the Prosobranchia at the side or behind. Given off from the apex of the ventricle is a large vessel which soon bifurcates to form anterior and posterior aortæ. These are the main trunks of the arterial system, their finest branches terminate in sinuses.

The **nervous system** varies considerably in the different groups in regard to the arrangement of the ganglia and their commissures and connectives.

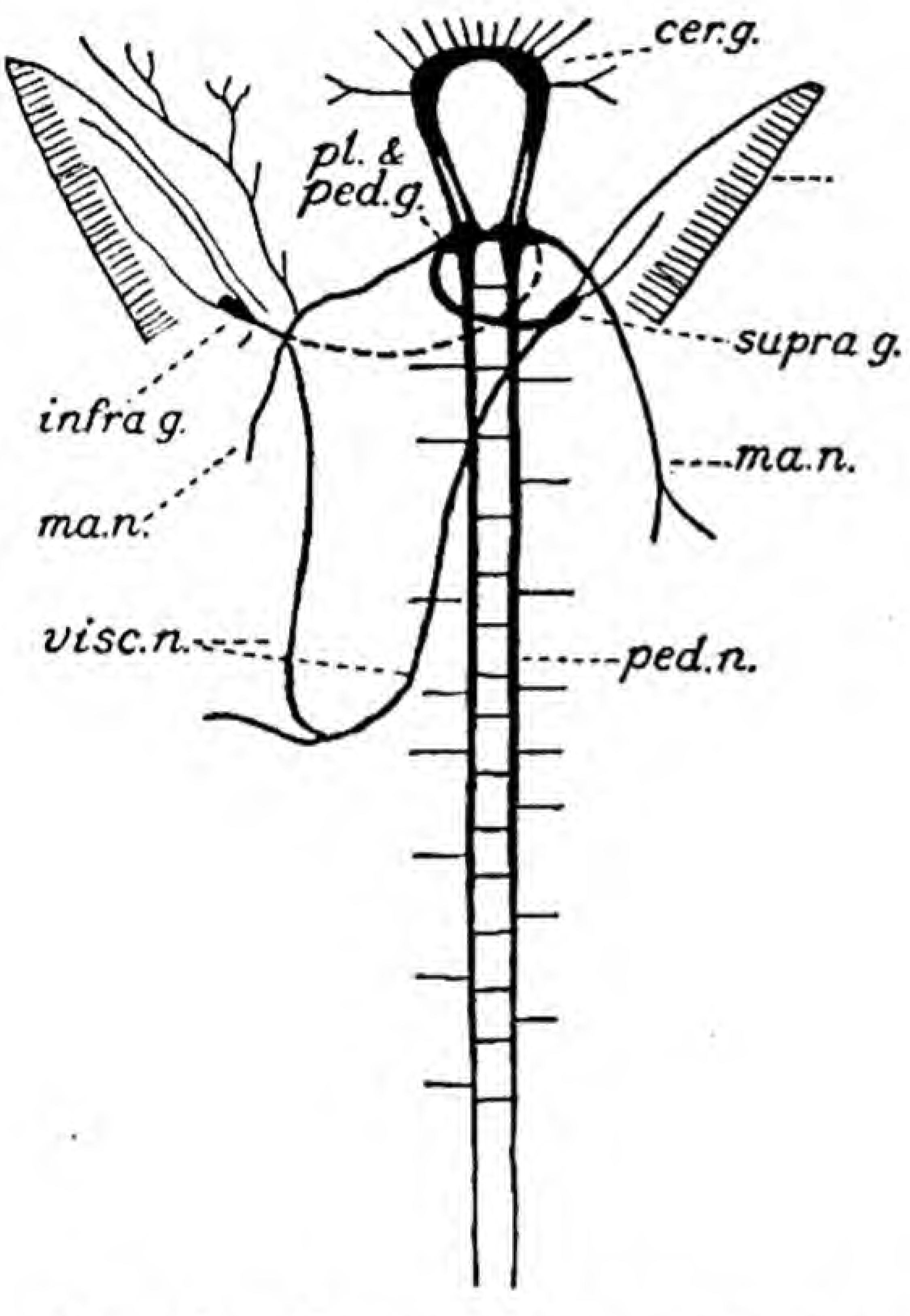


Fig. 564.—Nervous system of **Haliotis.** *cer. g.*, cerebral ganglion; *ct.* ctenidium; *infra g.*, infra-intestinal parietal ganglion; *ma. n.*, mantle nerve; *ped. n.* pedal nerve; *pl. and ped. g.*, pleural and pedal ganglia; *supra g.*, supra intestinal parietal ganglion; *visc. n.*, visceral nerve. (From Shipley and MacBride's *Zoology* (Cambridge University Press), after Lacaze-Duthiers.)

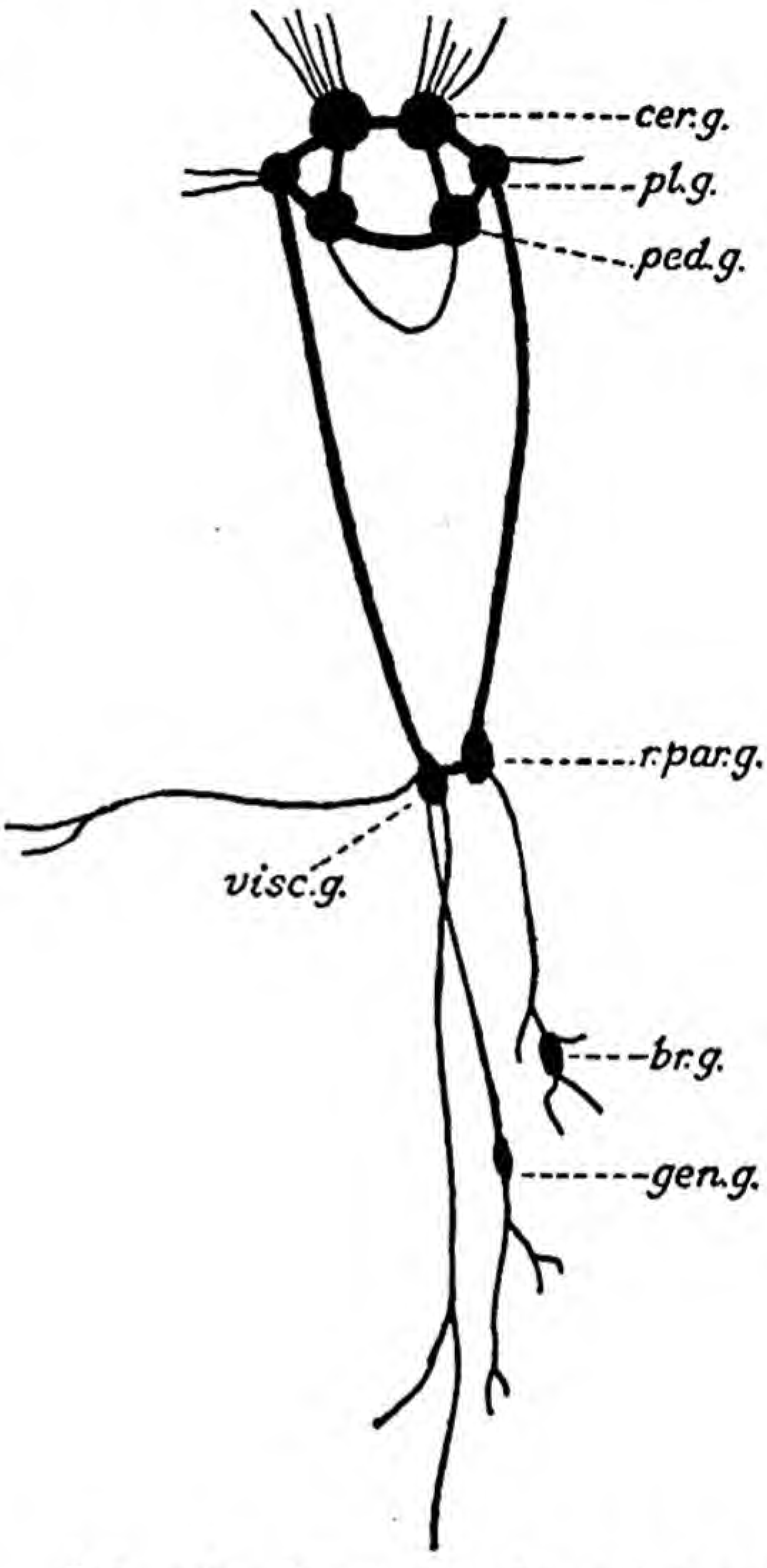


Fig. 565.—Nervous system of **Aplysia** (Opisthobranchia). *br. g.*, branchial ganglion; *cer. g.*, cerebral ganglion; *gen. g.*, genital ganglion; *ped. g.*, pedal ganglion; *pl. g.*, pleural ganglion; *r. par. g.*, right parietal ganglion; *visc. g.*, visceral ganglion. (After Eales.)

In the majority the arrangement is nearly that which has been described as occurring in Triton. There is a pair of *cerebral ganglia* usually closely united and situated over the gullet, and giving off behind a pair of nerve-cords, in the course of which there is placed laterally a pair of *pleural ganglia*, and which are united together behind in a *median visceral ganglion* (or a paired ganglion, as in Triton). In the course of these cords there is also a pair of *parietal*

ganglia. A pair of *pedal ganglia*, united together by a transverse commissure and joined to the cerebral and pleural ganglia by connectives, may give off behind one or two pairs of pedal nerves. A pair of *buccal ganglia* are connected by slender nerves with the cerebral. At the base of each osphradium is usually a small *osphradial ganglion* connected by a slender nerve with the parietal. In most Prosobranchia (Fig. 547), in accordance with the torsion of the visceral mass, the visceral cords are twisted, as already described in the case of Triton, into a figure of 8 : the right parietal ganglion becomes displaced to the left and comes to lie above the alimentary canal (supra-intestinal), while the left becomes displaced to the right and comes to lie below the alimentary canal (infra-intestinal).

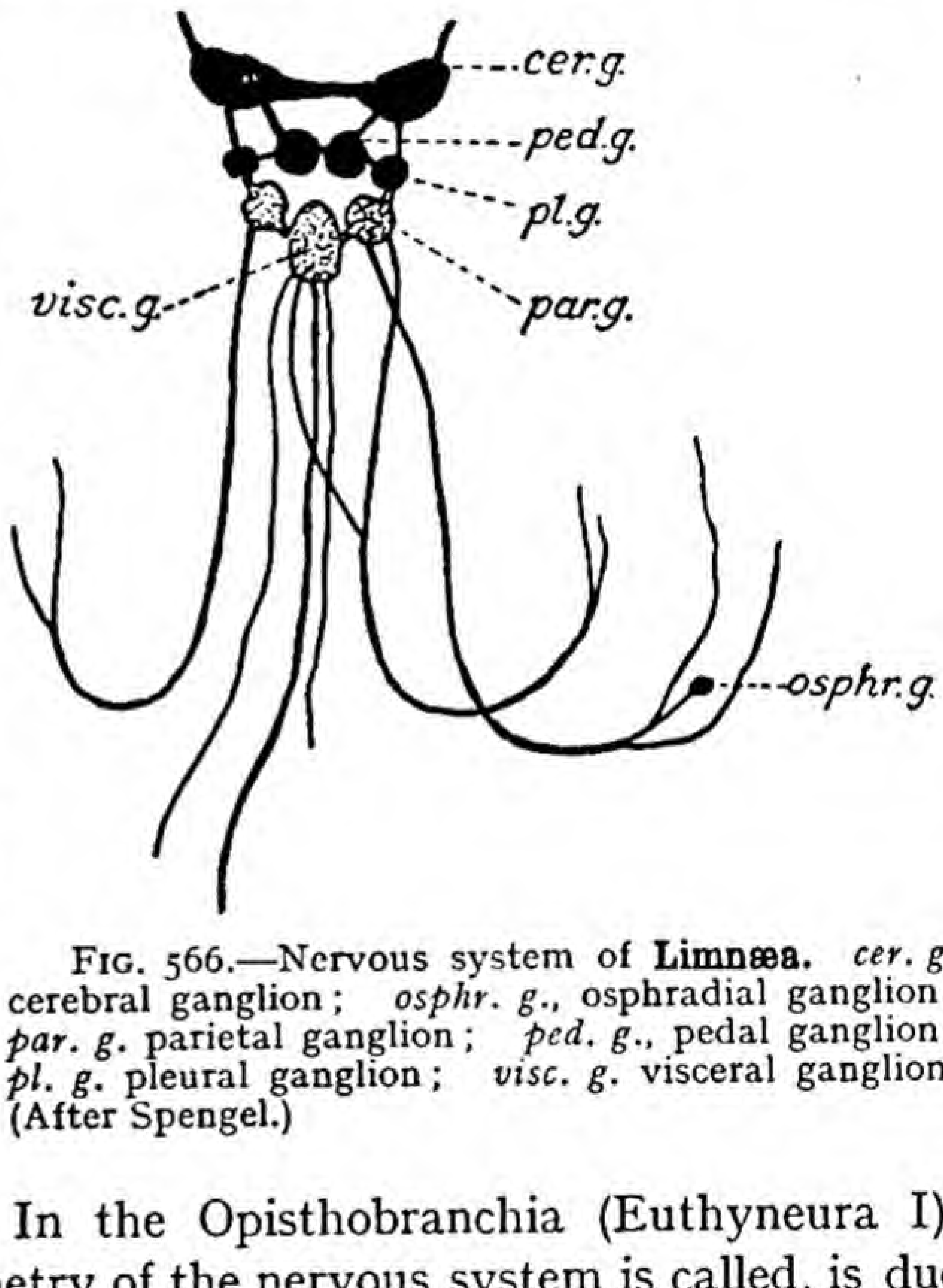


FIG. 566.—Nervous system of **Limnæa.** *cer. g.* cerebral ganglion; *osphr. g.*, osphradial ganglion; *par. g.* parietal ganglion; *ped. g.*, pedal ganglion; *pl. g.* pleural ganglion; *visc. g.* visceral ganglion. (After Spengel.)

In Haliotis (Fig. 564) and Fissurella the united pleural and pedal ganglia (*pl.* and *ped. g.*), give origin to a pair of elongated pedal nerve-cords (*ped. n.*), which are connected together by transverse commissures, and, in the latter genus, join one another posteriorly.

In the Opisthobranchia (Fig. 565) and in the Pulmonata (Fig. 566)—except in Actæon (Opisthobranchia) and Chilina (Pulmonata)—the visceral loop is not caught up in the twist of the visceral mass. The symmetry of the nervous system in these Gastropods is a secondary one. In the Opisthobranchia (Euthyneura I), *euthyneury*, as this secondary symmetry of the nervous system is called, is due to the untwisting of the visceral loop caused by detorsion. In *Aplysia* (Fig. 565) the connective between the visceral ganglion and the supra-intestinal (primitively right) parietal ganglion is very short. The infra-intestinal (primitively left) parietal ganglion has disappeared.

In the Pulmonata (Euthyneura II) the secondary symmetry (euthyneury) is due to a shortening of the connectives making up the visceral loop. In *Limnæa* (Fig. 566) a pair of cerebral ganglia overlie the œsophagus, and below it is a mass of ganglia in which are to be made out a pair of pedal ganglia and two pairs of ganglia representing the pleural and parietal ganglia. There is also a visceral ganglion.

The **sense-organs** are the eyes, the statocysts, and the osphradia. In nearly

all cases there are two cephalic *eyes* (Fig. 567), the position of which has already been referred to in the account given of the external characters. In structure they are simplest in *Patella* (*A*), where each consists of a pit-like depression, lined by pigmented cells connected with nerve-fibres. In the majority they have the structure described in the case of Triton. In certain species of *Oncidium*, a littoral Pulmonate, there are numerous eyes of a simple type scattered over the dorsal surface. In this case the optic nerve pierces the retina and the cells of the latter have their free ends directed away from the centre of

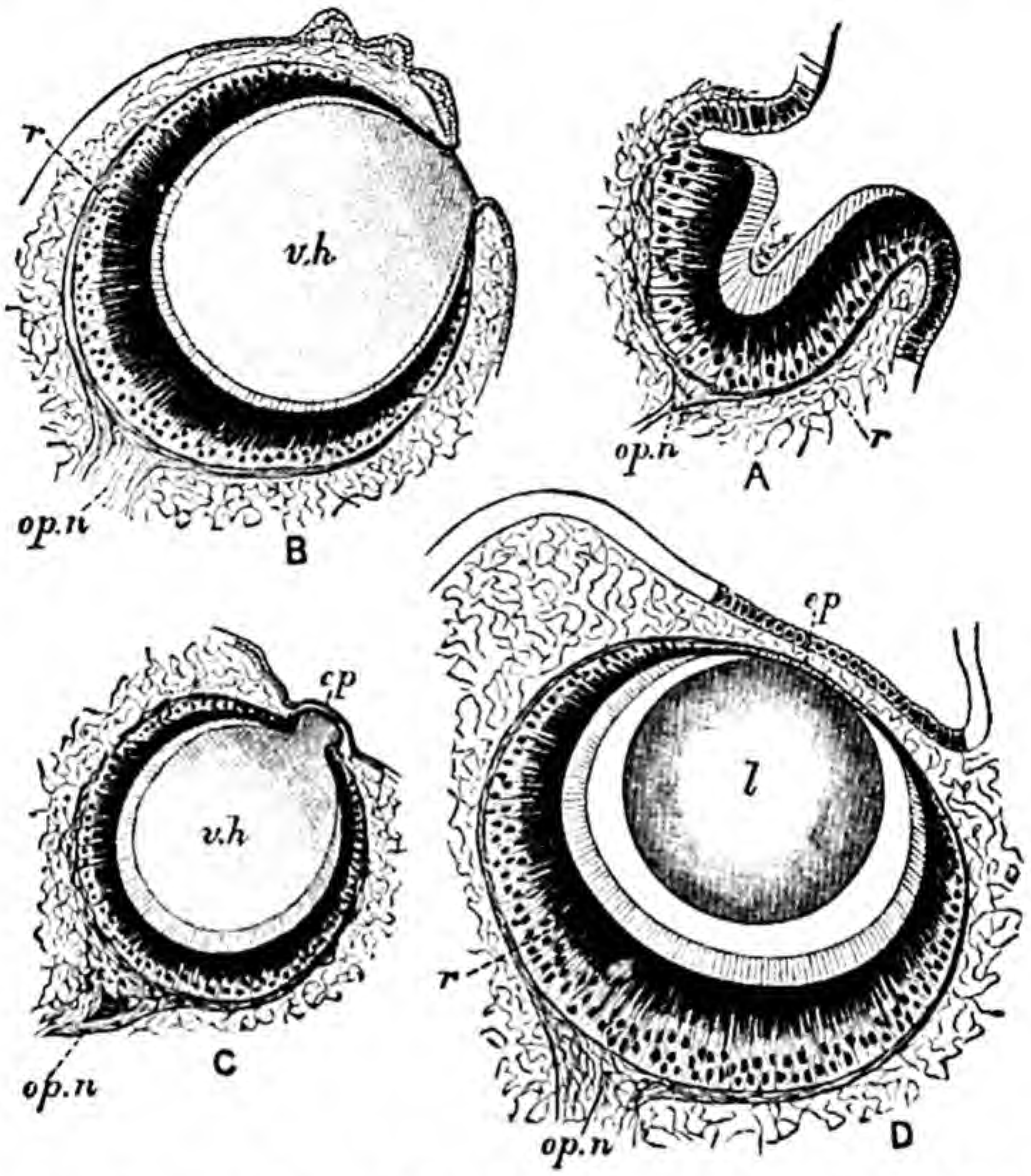


FIG. 567.—Eyes of Gastropoda. *A*, **Patella**; *B*, **Trochus**; *C*, **Turbo**; *D*, **Murex**. *ep*. epidermis; *l*. lens; *op. n*. optic nerve; *r*. retina; *v. h*. vitreous humour. (From the *Cambridge Natural History*, after Helger.)

the eye, as in the Bivalve *Pecten* (see Fig. 609, p. 606) and in the Vertebrata, instead of towards it, as in other Mollusca. The internal cavity of the eye in *Oncidium* is occupied by a refractive body composed of a few large transparent cells.

The *statocysts* are usually placed in close relation to the pedal ganglia, but are always innervated from the cerebral. An *olfactory organ* is present in the shape of groups of cells on the tentacles, in which the fibres of an olfactory nerve terminate.

The *osphradia* are prominences, usually of simple form, situated close to the base of the ctenidium. In many of the branchiate Prosobranchia, as

already mentioned in the case of Triton (see p. 549, Fig. 541), the primitively right osphradium, which is alone developed, assumes the form of a pectinate body with a central ridge, on either side of which is a row of close-set lateral laminæ, and is commonly termed the *parabranchia*, from its resemblance in appearance to a gill. In some cases it is of even more complicated shape than in Triton, owing to the branching of the lateral ridges.

The **excretory organs** or **kidneys** of the Gastropoda are dorsally placed glandular tubes or chambers, which communicate internally with the pericardium, and open on the exterior, either directly or through a duct—the *ureter*. Both right and left kidneys may be present, though unequal in size, the one situated to the right of the anus being larger than that situated to the left; or the former may alone be developed. In a very limited number of Gastropoda the gonad opens into the kidney.

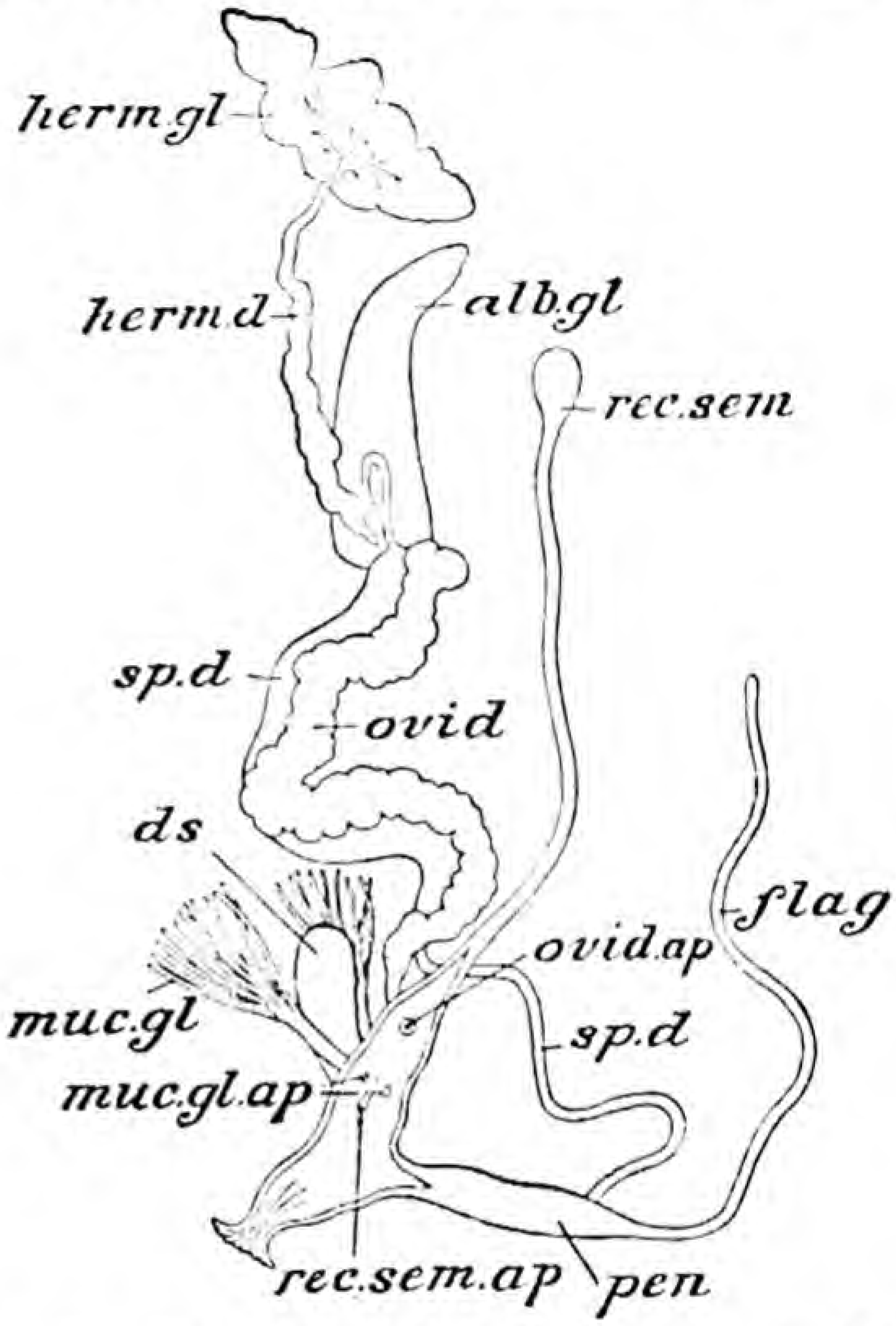


FIG. 568.—Reproductive organs of **Helix.** *alb.gl.* albumen-gland; *ds.* dart-sac; *flag.* flagellum of the penis; *herm. gl.* hermaphrodite gland or ovotestis; *herm. d.* duct of hermaphrodite gland; *muc. gl.* mucous gland; *muc. gl. ap.* apertures of mucous glands into vestibule; *obid.* oviducal part of the common duct; *ovid. ap.* apertures of oviduct into vestibule; *pen.* penis; *rec. sem.* receptaculum seminis; *rec. sem. ap.* aperture of receptaculum seminis; *sp. d.* sperm duct; *sp. d'.* spermiducal part of common duct. (After Pelseneer.)

The **sexes** are separate in nearly all the Prosobranchia, united in the Opisthobranchia and Pulmonata. Special gonoducts are present, except in one or two forms in which the kidneys perform that function. In the unisexual forms the reproductive apparatus is of a comparatively simple character, consisting merely of a racemose reproductive organ, ovary or testis as the case may be, situated dorsally in the visceral spiral, with the gonoduct opening far forwards on the right-hand side, and, in the male, a penis, which is grooved longitudinally and non-retractile. In the hermaphrodite forms, such as the Pulmonata (Fig. 568), on the other hand, a considerable degree of complexity is observable. There are a *hermaphrodite gland* (*herm. gl.*, Fig. 569, *A*)—some of the follicles of which produce ova while others produce sperms, a convoluted *hermaphrodite duct* (*herm. d.*), an albumen-gland, in which the albumen of the relatively large eggs is formed, and sometimes a separate oviduct and sperm-duct leading to a common genital opening; sometimes there

is a single duct undivided throughout; sometimes there is incomplete division. A receptaculum seminis (*rec. sem.*) is connected with the oviduct, and also a number of narrow accessory oviducal glands (*muc. gl.*); frequently a gland termed *prostate* is connected with the sperm-duct, and there are an eversible sac—the *sac of the dart* (*ds.*)—containing a calcareous stylet, and a *penis* (*pen.*), which is perforated by a canal and is capable of being retracted by a special muscle. In the Pulmonata the first part of the duct (*hermaphrodite duct* proper) is simple, and serves for the passage of both ova and sperms: the middle part is incompletely divided internally into two passages, one serving as oviduct, the other as sperm-duct. In the distal part oviduct and sperm-duct are completely separate. Where the sperm-duct enters the penis, there is given off a long, slender, tapering diverticulum, the *flagellum* (*flag.*), in which the sperms are made up into elongated masses or *spermatophores*.

Development.—The Limpets (*Patella*) are exceptional in laying the eggs one

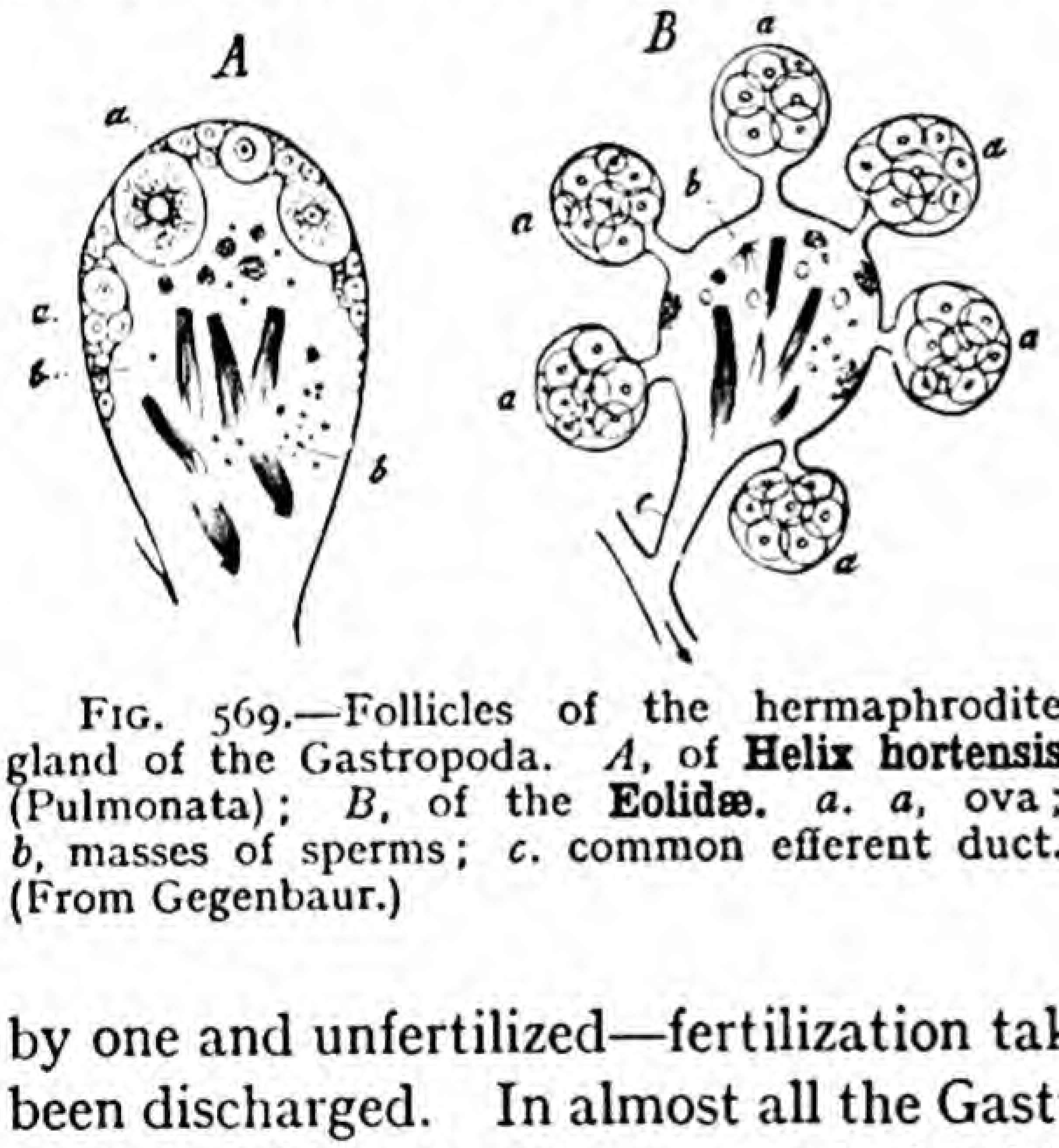


Fig. 569.—Follicles of the hermaphrodite gland of the Gastropoda. *A*, of **Helix hortensis** (Pulmonata); *B*, of the **Eolidæ**. *a. a*, ova; *b*, masses of sperms; *c*. common efferent duct. (From Gegenbaur.)

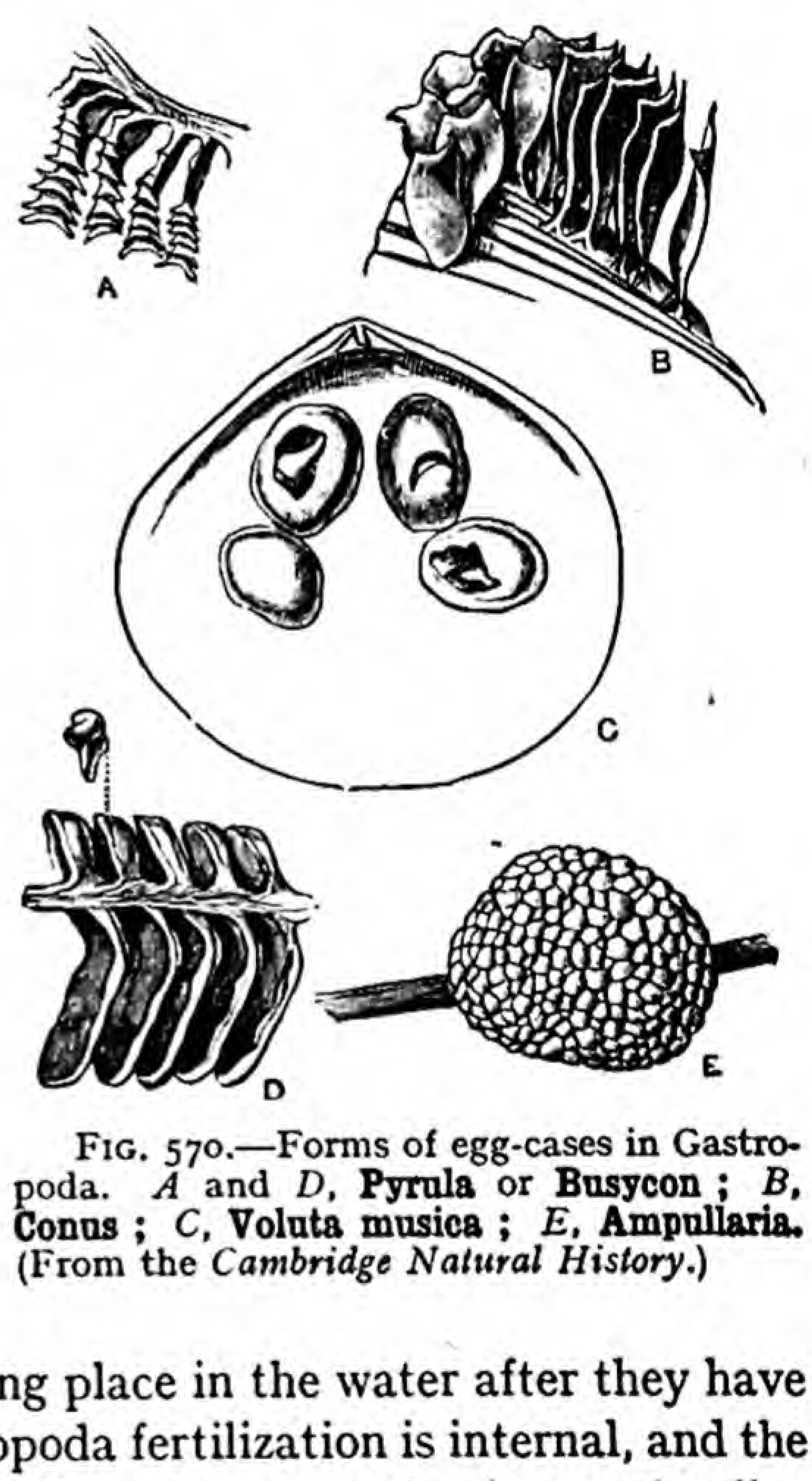


Fig. 570.—Forms of egg-cases in Gastropoda. *A* and *D*, **Pyrula** or **Busycon**; *B*, **Conus**; *C*, **Voluta musica**; *E*, **Ampullaria.** (From the *Cambridge Natural History*.)

by one and unfertilized—fertilization taking place in the water after they have been discharged. In almost all the Gastropoda fertilization is internal, and the eggs are laid in great masses, embedded in jelly, each egg having its own hyaline envelope. Very often the mass of spawn consisting of the jelly-like substance, with the eggs embedded in it, attains a relatively considerable size. In form it varies greatly: frequently it is in the shape of long strings which are cylindrical or band-like: sometimes several such strings are twisted together into a cord. Sometimes the spawn is fixed to sea-weed or other objects; sometimes it is unattached, and may float about freely. In the Prosobranchia (Fig. 570), instead of being embedded in a jelly-like mass, the eggs are enclosed

in a firm parchment-like capsule, in which is contained, in addition to the eggs, a quantity of an albuminous fluid, serving to nourish the developing embryos. The shape of the capsule varies greatly in the different genera : sometimes it is stalked, sometimes sessile ; in some cases there is a lid or operculum, the opening of which permits the embryos to escape. Very commonly large numbers of these capsules are aggregated together, and usually they are attached to a rock or a sea-weed or similar object. In many cases only a limited number—some-

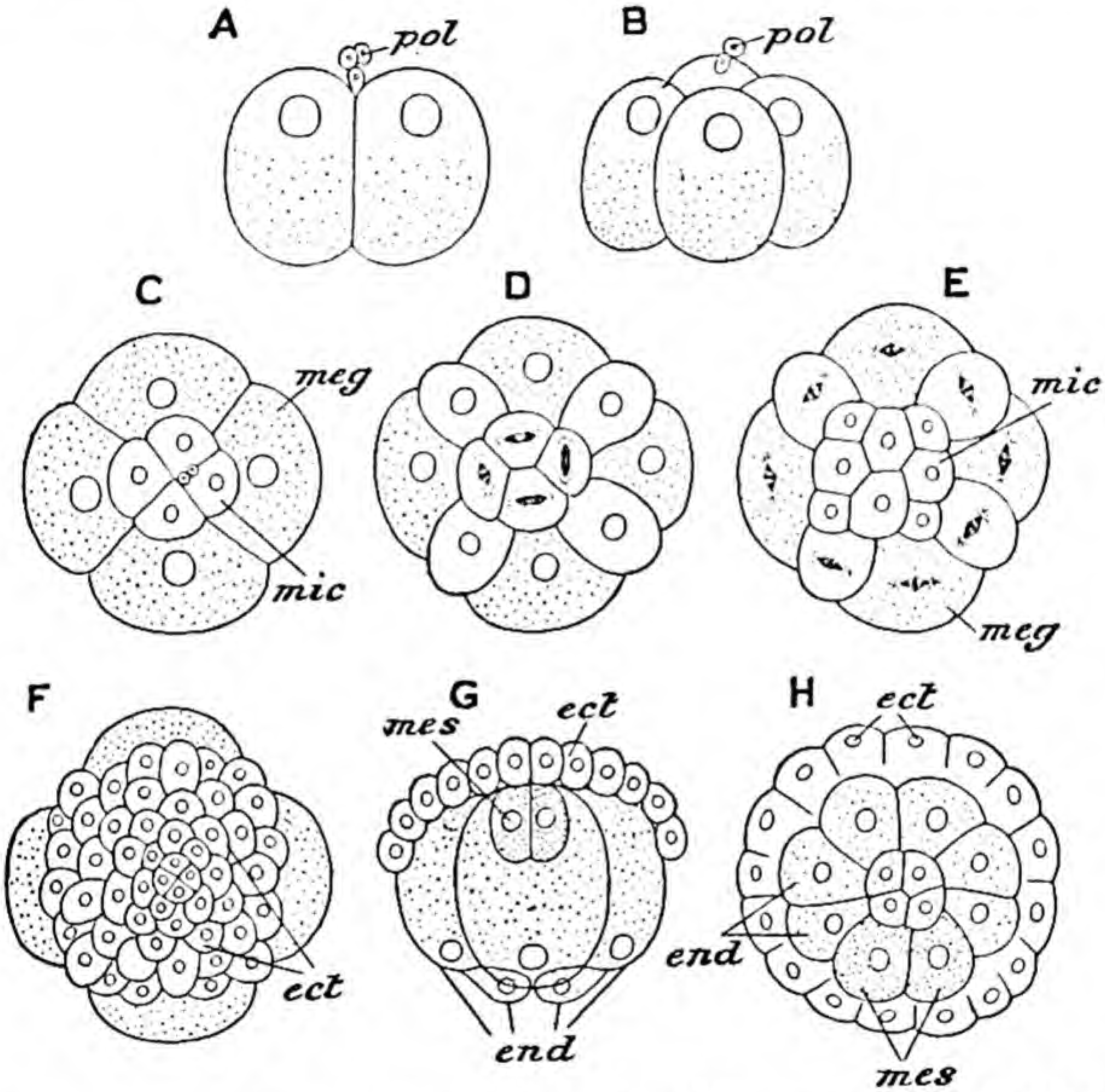


FIG. 571.—Diagram of the cleavage and formation of the germinal layers of the Gastropoda. *A* and *B*, lateral view ; *C—F*, viewed from the animal (upper) pole ; *H*, from the vegetative (lower) pole ; *G*, in optical section ; *ect.* ectoderm ; *end.* endoderm ; *mic.* micromeres ; *meg.* macromeres ; *mes.* mesoderm ; *pol.* polar bodies. (After Korschelt and Heider.)

times only one—of the embryos contained in the capsule become developed, the rest serving as nutriment for the survivors.

In the land Pulmonata each ovum may be embedded in gelatinous matter enclosed in a firmer envelope, and a number of them are arranged in a string; sometimes a large number are embedded in a rounded gelatinous mass. Usually as in some species of *Helix* and other genera, the outer layers of the albumen-like substance enclosing the egg become toughened and impregnated with salts of lime, so as to assume the character of a calcareous shell ; a number of such

eggs, which are of relatively considerable size, are laid in holes excavated in the earth.

In a few marine and fresh-water Gastropoda the ova undergo their development in the body of the parent, enclosed in an enlargement of the oviduct which serves as a uterus.

The egg contains a considerable quantity of food-yolk, which may be evenly

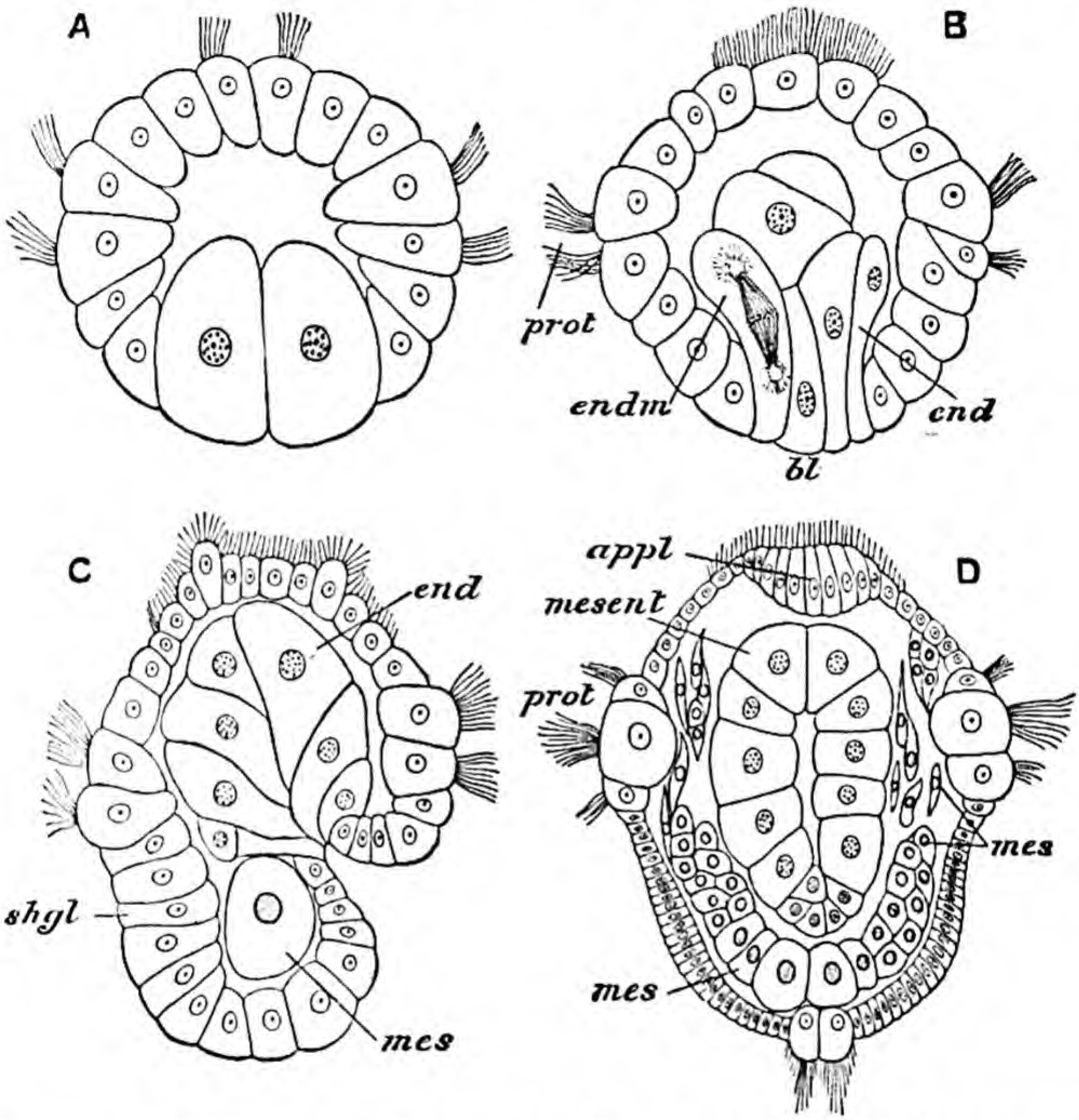


FIG. 572.—Earlier stages in the development of **Patella.** *A*, blastula; *B*, beginning of endodermal invagination; *C*, completion of gastrula; *D*, frontal section of somewhat later stage. *ap. pl.* apical plate; *bl.* blastopore; *endm.* endo-mesoderm cell; *end.* endoderm; *mes.* mesoderm; *mesent.* mesenteron; *prot.* prototroch; *sh. gl.* shell-gland. (From Korschelt and Heider, after Patten.)

distributed, or a clear protoplasmic and an opaque yolk-laden segment may be distinguishable. There is a fairly close agreement throughout the class in the nature of the cleavage (Fig. 571), which is a typical spiral cleavage, very similar in the early stages to that of *Nereis* and the Chætopoda in general (p. 319) and to that of a Polyclad (p. 253). In all cases it is total, sometimes equal at first, but soon afterwards becoming unequal. The first four blastomeres, *A*, *B*, *C*, *D*

(*cf.* Fig. 219), are usually equal or nearly so. From these a succession of four quartettes of smaller cells (*micromeres*) become divided off, the larger cells being the *macromeres*. The former then increase by division and form a cap of small cells (ectoderm) on the surface of the macromeres. Of the cells of the fourth quartette, three become endoderm cells, contributing to the endodermal lining of the mesenteron. The fourth becomes the parent cell of the mesoderm.

The macromeres themselves eventually become converted into endoderm cells with the exception of *D*, which, before becoming an endoderm cell, gives off internally its daughter-cell of the fourth quartette destined, as in the Polychæta (p. 320), to give rise to the mesoderm. A blastocœle is developed between the micromeres and the macromeres, and the result is the formation

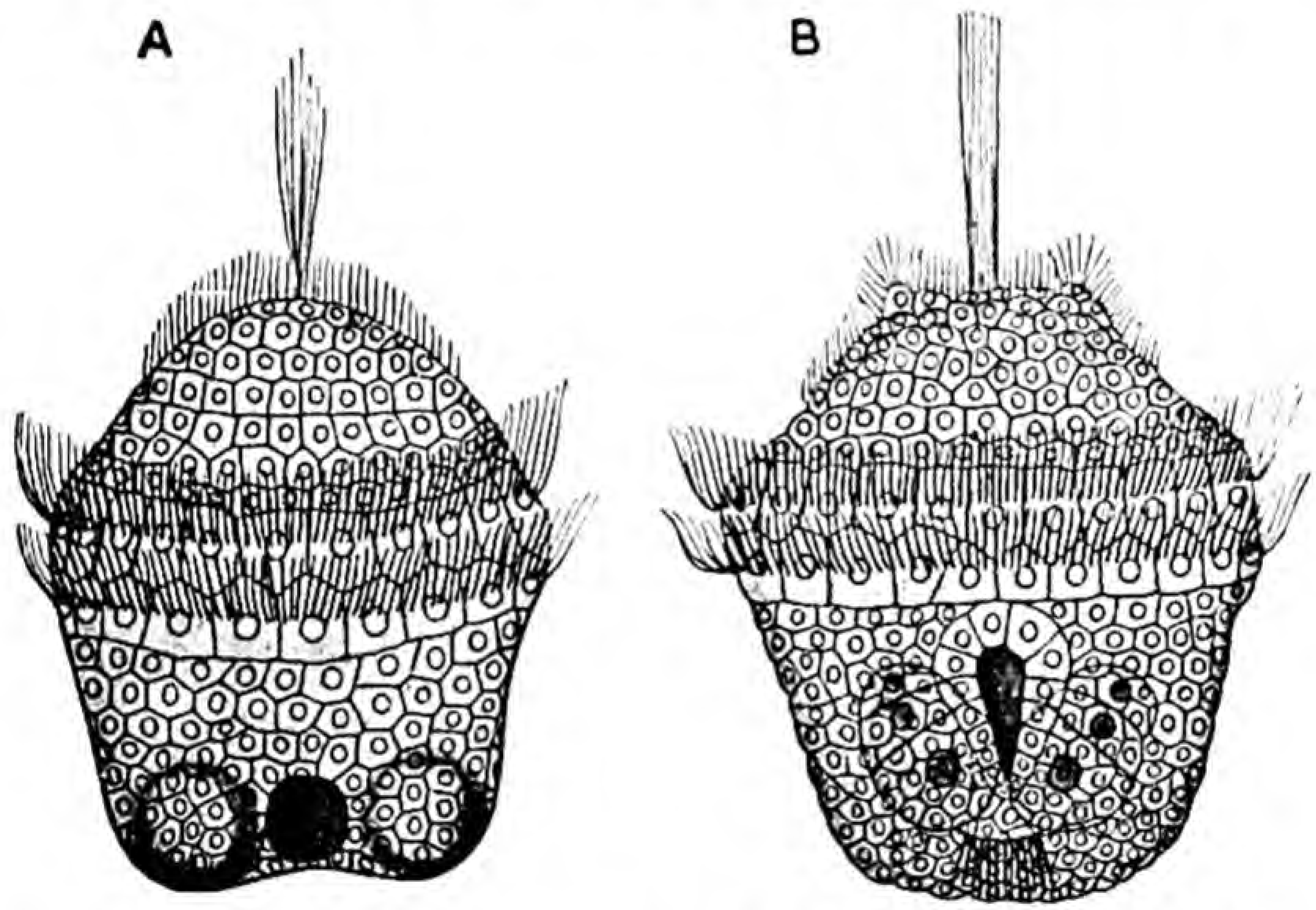


FIG. 573.—*A* and *B*, Trochophores of **Patella** at different stages. In *A* are to be seen the circular blastopore and the two foot-elevations; in *B* the blastopore is drawn out, at the sides of it are the two mesoderm bands. (From Korschelt and Heider, after Patten.)

of the blastula, one side of which (*vegetative pole*) is greatly thickened owing to its consisting of the large macromeres, the opposite side (*animal pole*) being made up of micromes. This may become a gastrula by epiboly or over-growth of the ectoderm over the macromeres; or, if the blastocœle is of considerable size (*Paludina*), an invagination takes place.

The two larval stages, the *trochophore* and the *veliger*, are characteristic of the development of the Gastropoda. The former is most typically developed in *Patella*; in other Gastropods it undergoes more or less modification. In Patella (Fig. 572) there is a ciliated blastula (*A*) which has on one side the large macromeres. The latter become enclosed by the micromeres, and the foundation of the mesoderm is laid in the manner already described. The blastopore is situated at the vegetative pole, destined to become the hinder end of the larva, but it soon changes its position, and extends forwards on the ventral

side, and a ciliated ring—the *prototroch* or future *velum*—is formed. Subsequently the position of the blastopore becomes still further shifted and its form U-shaped and then slit-like. It undergoes elongation (Fig. 573, *A*) and eventually becomes partly closed up, the closure taking place from behind forwards; in most cases in the position of the anterior part a sinking-in of the ectoderm forms the rudiment of the stomodæum. The originally solid mass of endoderm develops a lumen, and its cells become arranged to form the enteric epithelium. From the posterior end, where the mesoderm cells are situated, proceed two very regularly formed mesoderm-bands (Fig. 573, *B*). On the dorsal surface the shell-gland has already appeared as a pit lined by elongated ectoderm cells; on the surface of this appears the embryonic shell. The rudiment of the foot (Fig. 573, *A*) arises at a remarkably early stage as two protuberances lying on the ventral side of the posterior end of the larva at the sides of the blastopore; these coalesce to form the median foot.

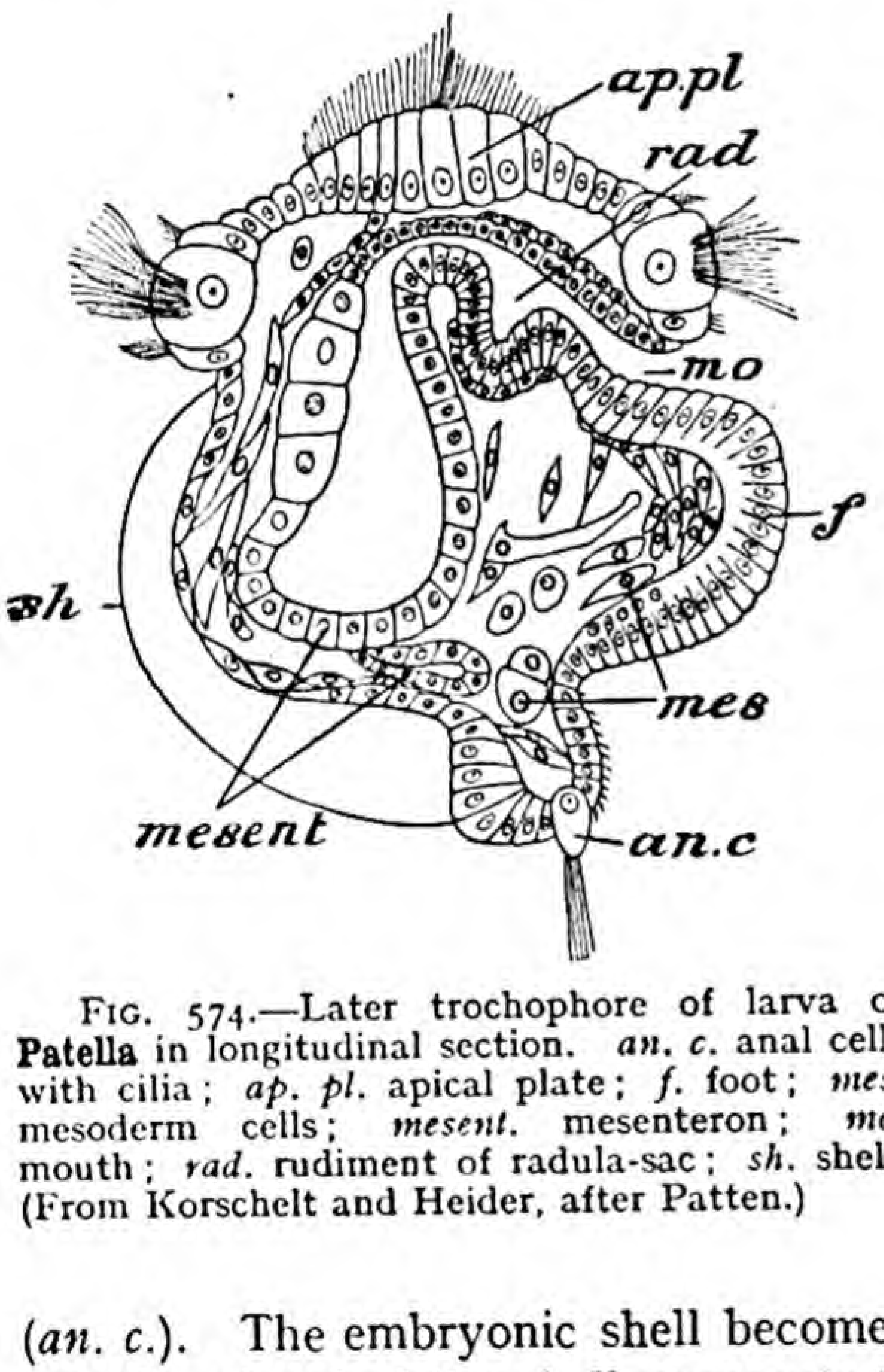


FIG. 574.—Later trochophore of larva of **Patella** in longitudinal section. *an. c.* anal cells with cilia; *ap. pl.* apical plate; *f.* foot; *mes.* mesoderm cells; *mesent.* mesenteron; *mo.* mouth; *rad.* rudiment of radula-sac; *sh.* shell. (From Korschelt and Heider, after Patten.)

The larva (Fig. 574) has now assumed the trochophore form. The pre-oral part is large and convex, with an apical plate on which is borne a bunch of long cilia, and near it two small ciliated elevations, each consisting of a single cell. The pre-oral part of the larva then becomes much flattened, and the apical plate (*ap. pl.*) increases in size and importance. At the posterior end is a bunch of cilia which are borne on two special large cells, the *anal cells* (*an. c.*). The embryonic shell becomes saucer-shaped. A slight ridge in the neighbourhood of the shell represents the border of the mantle. The mid-gut (*mesent.*) has become considerably widened: a diverticulum from it is recognizable, and this afterwards opens on the exterior to form the anus. A diverticulum of the fore-gut (*rad.*) at the same time forms the rudiment of the radular sac. The statolith-sacs appear as depressions of the ectoderm at the sides of the mouth: these grow inwards and become sac-like, subsequently lying at the sides of the foot, which has meantime attained a considerable size.

The trochopore-stage, which is so well marked in the case of *Patella*, occurs in other Gastropods, though, as a rule, presenting modifications perhaps trace-

able to the enclosure of the embryo in an egg-shell and to the presence of much food-yolk. The history of the blastopore is not the same in all cases; in *Paludina* it is said to become converted into the anus; in some the mouth is developed from its anterior portion; in others the stomodæal invagination arises after its complete closure, or may, with the mantle-cavity, only become developed after the symmetry has been disturbed by torsion. In most of the Gastropoda the pre-oral circlet or velum (Fig. 575, *vel.*) becomes greatly extended as a bilobed flap, the strong cilia with which it is bordered rendering it a very efficient organ of locomotion for the larva. With the full development of the velum the larva passes into the veliger stage (Fig. 575). In this stage the shell (*sh.*) increases in size, loses its simple form, and begins to develop

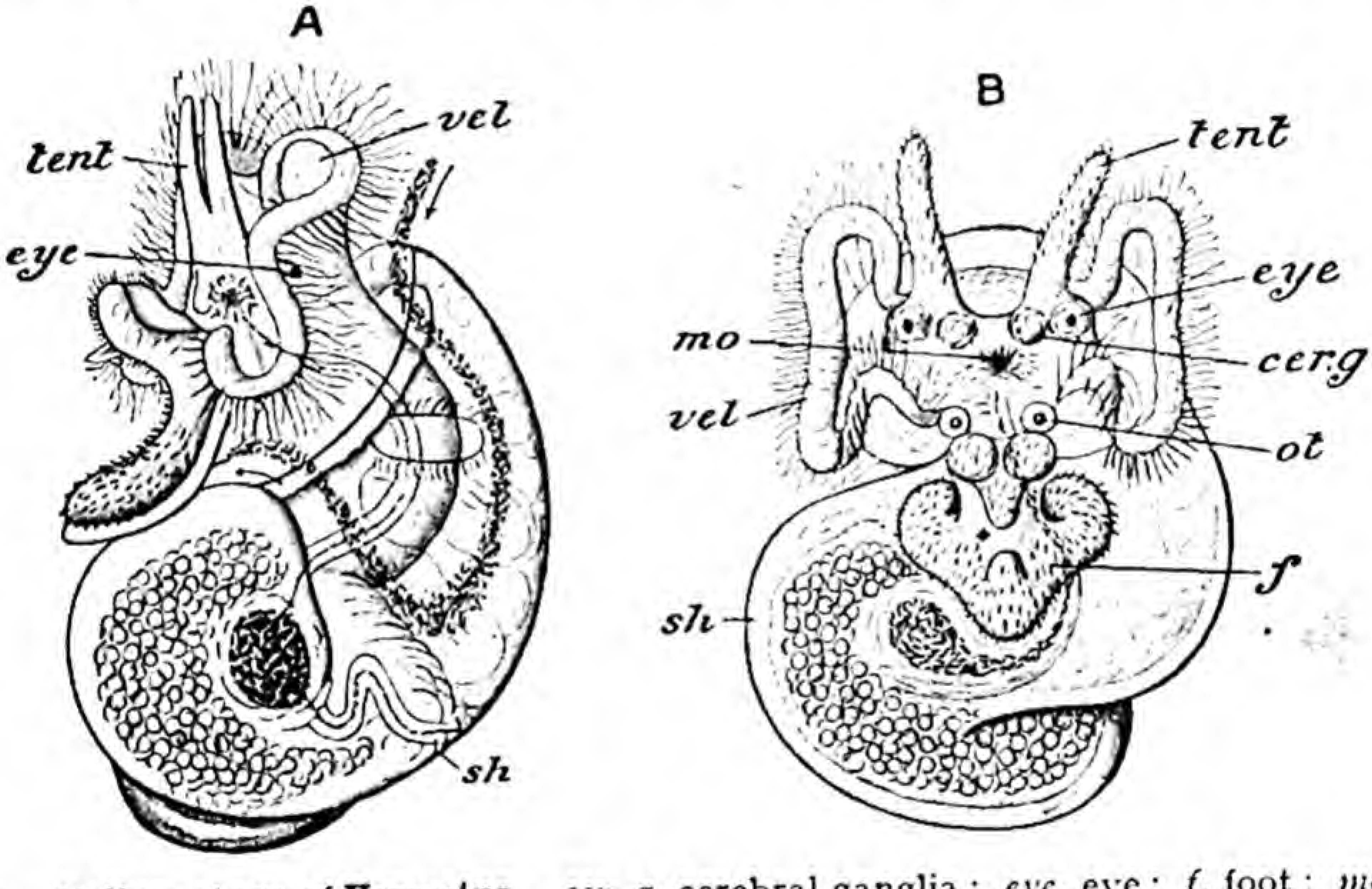


FIG. 575.—Veliger stage of **Vermetus.** *cer. g.* cerebral ganglia; *eye*, eye; *f.* foot; *mo.* mouth; *ot.* statocyst; *sh.* shell; *tent.* tentacle; *vel.* velum. (After Lacaze-Duthiers.)

a spiral. A cleft-like depression in the border of the mantle on the right-hand side forms the rudiment of the mantle-cavity in which, later, the gills are developed. The anus when it first appears may be symmetrically placed, but later becomes shifted to the right side and forwards as well as dorsally. A pair of cœlomoducts are developed, having some resemblance to the larval nephridia of the trochophore of Polychæta, being, however, of mesodermal origin. Each consists of a longer or shorter tube, usually intra-cellular, opening on the exterior at one end, and at the other terminating in one or several solenocytes. The foot (*f.*) may attain a considerable development during the veliger stage, and on its posterior and dorsal part appears the operculum. Two little processes on the velar area develop into the tentacles (*tent.*), and the eyes (*eye*) appear at their bases. As the foot and other organs advance in development the velum decreases in size and gradually aborts, but in some

cases a portion of it persists as the subtentacular lobes or labial tentacles in the neighbourhood of the mouth.

In the Pulmonata the velum is not well developed, except in Oncidium, though the trochophore stage is well marked.

The young Gastropod is at first bilaterally symmetrical; the prevailing asymmetry is the result of unequal growth of the two sides of the body. In the majority of cases it is the left side that grows more actively than the right, a result of which is that the posterior parts—the anus and the region surrounding it—are displaced forwards towards the right, the space between the anus and the mouth on that side undergoing little or no increase in length.

Modes of Life and Distribution.—Only a few aberrant families of Gastropoda are parasites. Most are aquatic, all the most primitive forms being inhabitants of the sea. Of the marine families the majority move by creeping over the sea-bottom, some burrowing in mud or sand, some in solid rock; some are able to float in a reversed position, adhering to frothy mucus secreted by the glands of the foot; certain exceptional forms such as *Vermetus* are fixed in the adult condition by the substance of the shell. A few families—the Heteropoda and the Pteropoda—are specially modified for a pelagic mode of existence, and swim through the water by flapping movements of the lobes of the foot, which act as fins. Gastropods are found in the ocean at considerable depths—down to nearly 3,000 fathoms. Many forms, however, are inhabitants of fresh-water, while many Pulmonata are terrestrial, and occur even towards the summits of the highest mountains.

Fossil Gastropoda are known from the Lower Cambrian, and, if the problematical Conularida are accepted as Pteropods, all the major divisions of the class are represented in formations of Palæozoic age, except the Heteropoda and Nudibranchia, which are unsuited for preservation as fossils.

CLASS IV.—SCAPHOPODA.

The Scaphopoda or Elephant's tusk-shells are aberrant marine Molluscs comprising only three Recent genera—*Dentalium, Siphonodentalium,* and *Pulsellum.* Fossil forms are found as far back as the Ordovician. The body is elongated so as to be almost worm-like, with complete bilateral cylindrical tube enclosed by the shell (Fig. 576), which is in the form of a delicate, curved tube, open at both ends and wider at the anterior or oral end than at the other. The foot (Fig. 577, *f.*) is narrow, trilobed at the extremity or provided with a terminal disc, capable of being protruded through the oral opening of the shell, and used for burrowing in sand. The mouth is situated

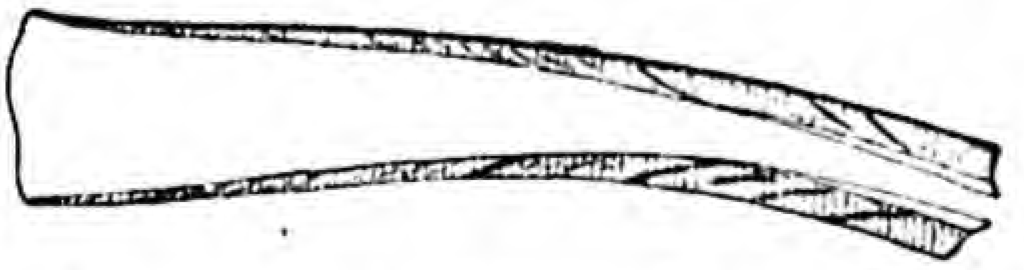


FIG. 576.—**Dentalium,** longitudinal section of shell. (After Keferstein.)

on a short oral proboscis, and is sometimes surrounded by lobed processes or pinnate palpi. Farther back are a pair of tentaculiferous lobes, each bearing a large number of filiform tentacles, which have a sensory function. The mouth leads into a buccal cavity containing an odontophore. Connected with the mesenteron is a large bilobed digestive gland (*l.*). The anus is situated ventrally behind the base of the foot. The vascular system is extremely simple, consisting of sinuses without definite walls, and there is no distinct heart, though in the neighbourhood of the rectum there is a specially contractile part of the principal sinus. Two tubes open near the anus, the right one acting as a gonoduct, the left (*k*) entirely renal in function. The sexes are distinct. There is an elongated unpaired gonad (*g.*), divided by lateral incisions into a number of lobes, occupying all the posterior and dorsal parts of the body. Anteriorly it narrows to form the gonoduct.

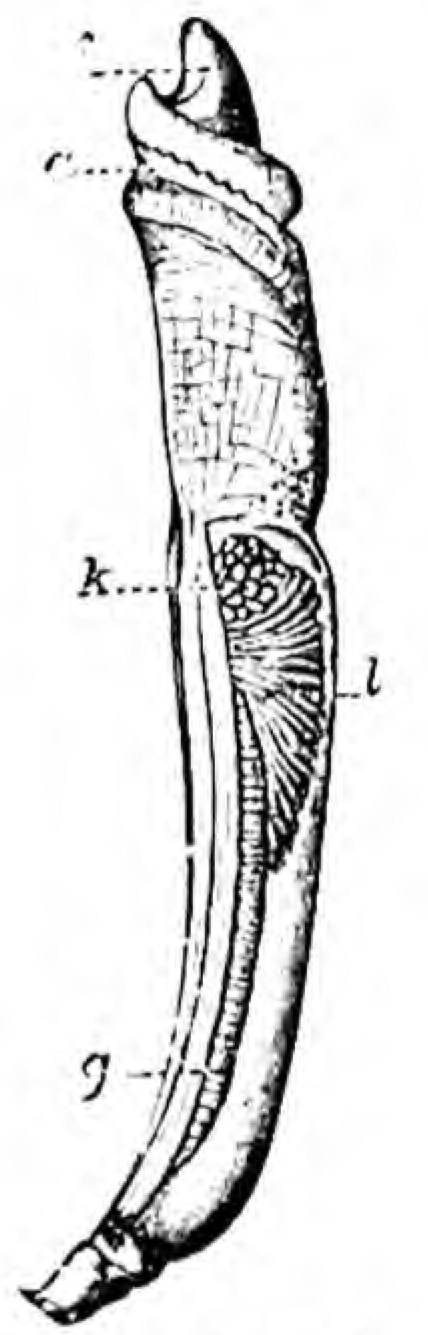


FIG. 577.—**Dentalium.** Anatomy. *a.* anterior aperture of mantle; *f.* foot; *g.* gonad; *k.* kidney; *l.* digestive gland. (From the *Cambridge Natural History*, after Lazace-Duthiers.)

The nervous system consists of paired cerebral, pleural, pedal, and visceral ganglia; the cerebral ganglia are situated close together. There are statocysts, but eyes are missing.

In the gastrula stage the embryo, which is provided with cilia, becomes free. The ciliated cells are arranged in a characteristic manner in three rows which, at first situated close together about the middle of the body, become shifted at a later stage near the apical pole, and amalgamated into a broad band representing the pre-oral circlet of other molluscan larvæ; at the same time a bunch of cilia previously developed at the apical pole becomes more conspicuous and a considerable part of the general surface covered with more delicate cilia. The blastopore, at first terminal, is shifted forwards on the ventral surface until it comes to be immediately behind the ciliated circlet. At its interior end an invagination gives rise to the mouth and stomodæum.

The larva (Fig. 578) has now attained the stage of a trochophore, in which, however, both apical plate and primitive excretory organs are wanting. A shell-gland is developed, and soon the rudiment of the shell appears. The post-oral region, at first inconsiderable in size, soon undergoes an increase, until it forms eventually by far the longest part of the body, while the pre-oral region almost completely aborts. When the post-oral region has attained a certain size, there are developed on it two lateral folds, the rudiments of the mantle (*B*), which grow inwards towards the middle ventral line, and later on unite by their free margins. The pre-oral circlet or velum changes its form—at first it is conical, later it becomes plate-like, and is then gradually

reduced, the larva sinking to the bottom; and though still occasionally swimming with the aid of the velum, coming to use the foot as a creeping organ. The shell now increases in size step by step with the growth of the mantle, and bends round the body of the larva until its edges meet and coalesce in

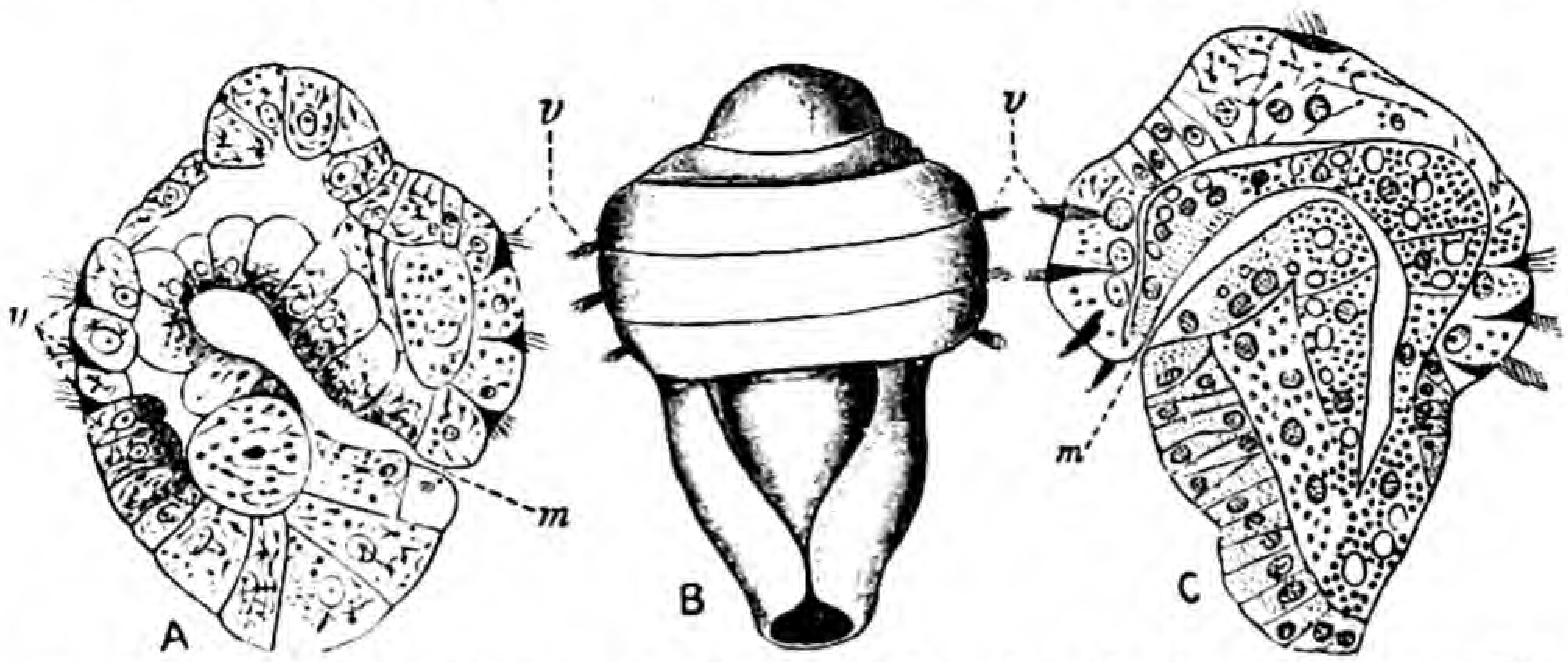


FIG. 578.—Veliger of **Dentalium.** *A*, longitudinal section of a larva 14 hours old; *B*, larva of 37 hours; *C*, longitudinal section of larva of 34 hours. *m.* mouth; *v*, *v*, velum. (From Cooke, after Kowalewsky.)

the ventral median line. Later it assumes the elongated conical form, curved towards the dorsal side, characteristic of the adult. The foot at the same time elongates and takes on the characteristic three-lobed shape. In some respects the Scaphopoda resemble primitive Bivalves.

CLASS V.—BIVALVIA (PELECYPODA).

1. Example of the Class—The Fresh-water Mussels (*Anodonta* and *Unio*).

Fresh-water Mussels are found in rivers and lakes in most parts of the world. *Anodonta cygnea*, the Swan-mussel, is the commonest species in England; but the Pearl-mussel, *Unio margaritifera*, is found in mountain streams, and other species of the same genus are universally distributed.

The Mussel (Fig. 579) is enclosed in a brown shell formed of two separate halves or *valves* hinged together along one edge. It lies on the bottom, partly buried in the mud or sand, with the valves slightly gaping, and in the narrow cleft thus formed a delicate, semi-transparent substance (*m.*) is seen—the edge of the *mantle* or *pallium*. The mantle really consists of separate halves or *lobes* corresponding with the valves of the shell, but in the position of rest the two lobes are so closely approximated as to appear simply like a membrane uniting the valves. At one end, however, the mantle projects between the valves in the form of two short tubes, one (*ex. sph.*) smooth-walled, the other (*in sph.*) beset with delicate processes or *fimbriæ*. By diffusing particles

of carmine or indigo in the water it can be seen that a current is always passing in at the fimbriated tube, hence called the *inhalant siphon*, and out at the smooth or *exhalant siphon*. Frequently a semi-transparent, tongue-like body (*ft.*) is protruded between the valves at the opposite side from the hinge and at the end farthest from the siphons: this is the *foot*; by its means the animal is able slowly to plough its way through the sand or mud. When the Mussel is irritated the foot and siphons are withdrawn and the valves tightly closed. In a dead animal, on the other hand, the shell always gapes, and it can then be seen that each valve is lined by the corresponding lobe of the mantle, and that the exhalant siphon is formed by the union of the lobes above and below it and is thus an actual tube; but that the boundary of the inhalant siphon facing the gape of the shell is simply formed by the approximation of the mantle-lobes, so that this tube is a temporary one.

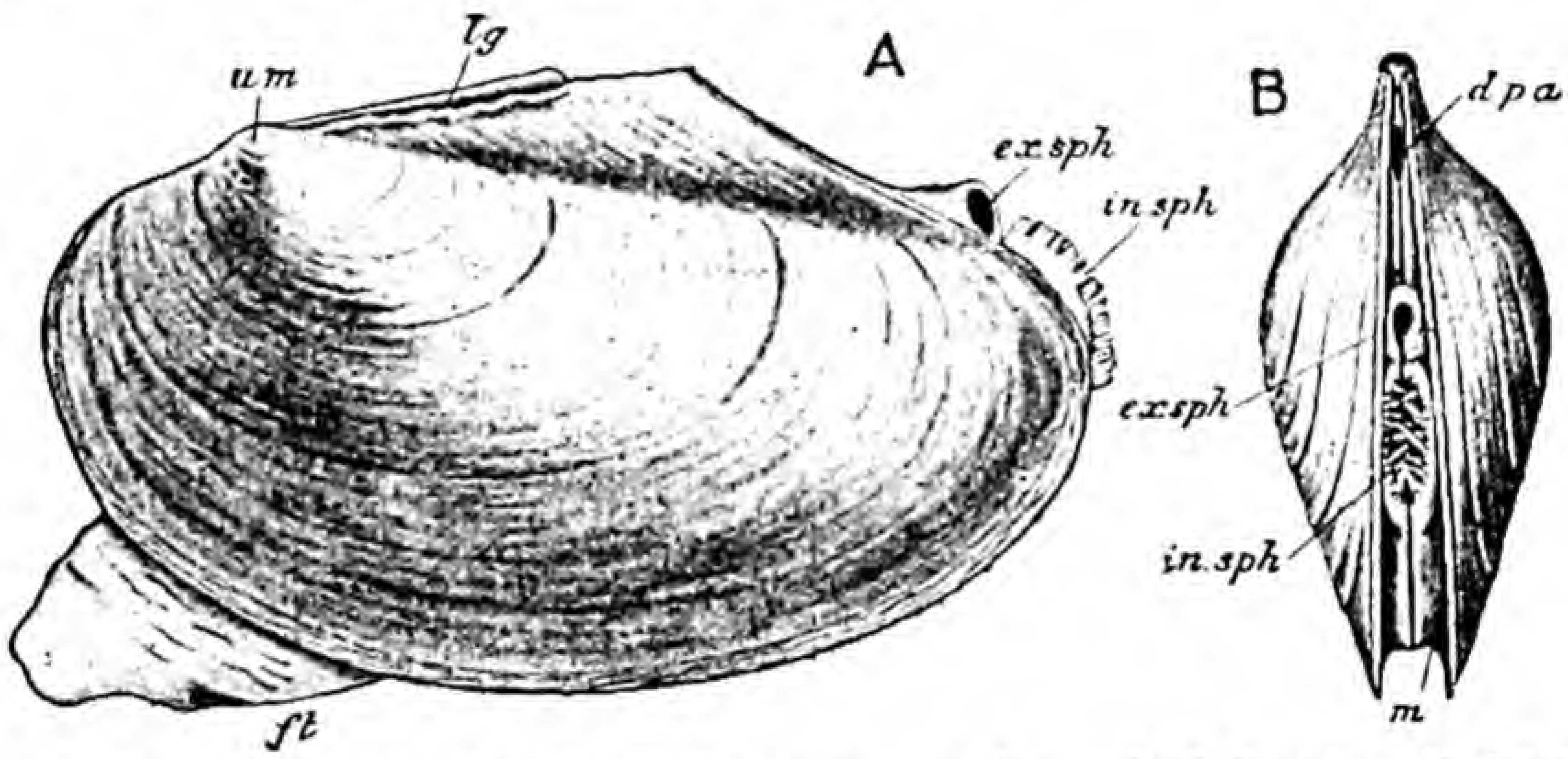


FIG. 579.—**Anodonta cygnea.** The entire animal. *A*, from the left side; *B*, from the posterior end. *d. p. a.* dorsal pallial aperture; *ex. sph.* exhalant siphon; *ft.* foot; *in. sph.* inhalant siphon; *lg.* ligament; *m.* mantle; *um.* umbo. (After Howes.)

The hinge of the shell is dorsal, the gape ventral, the end bearing the siphons posterior, the end from which the foot is protruded anterior; hence the valves and mantle-lobes are respectively right and left.

In a dead and gaping Mussel the general disposition of the parts of the animal is readily seen. The main part of the body lies between the dorsal ends of the valves; it is produced in the middle ventral line into the keel-like foot, and on each side, between the foot and the corresponding mantle-lobe, are two delicate, striated plates, the *gills* (Figs. 583–585). Thus the whole animal has been compared to a book, the back being represented by the hinge, the covers by the valves, the fly-leaves by the mantle-lobes, the first two and the last two pages by the gills, and the remainder of the leaves by the foot.

The Shell.—When the body of the mussel is removed from the shell the two valves are seen to be united, along a straight *hinge-line* (Fig. 580, *A*, *h.l.*), by a tough, elastic substance, the *hinge-ligament* (Figs. 579 and 585, *lg.*),

passing transversely from valve to valve. It is by the elasticity of this ligament that the shell is opened; it is closed, as we shall see, by muscular action: hence the mere relaxation of the muscles opens the shell. In Anodonta the only junction between the two valves is afforded by the ligament, but in Unio each is produced into strong projections and ridges, the *hinge-teeth*, separated by grooves or sockets, and so arranged that the teeth of one valve fit into the sockets of the other.

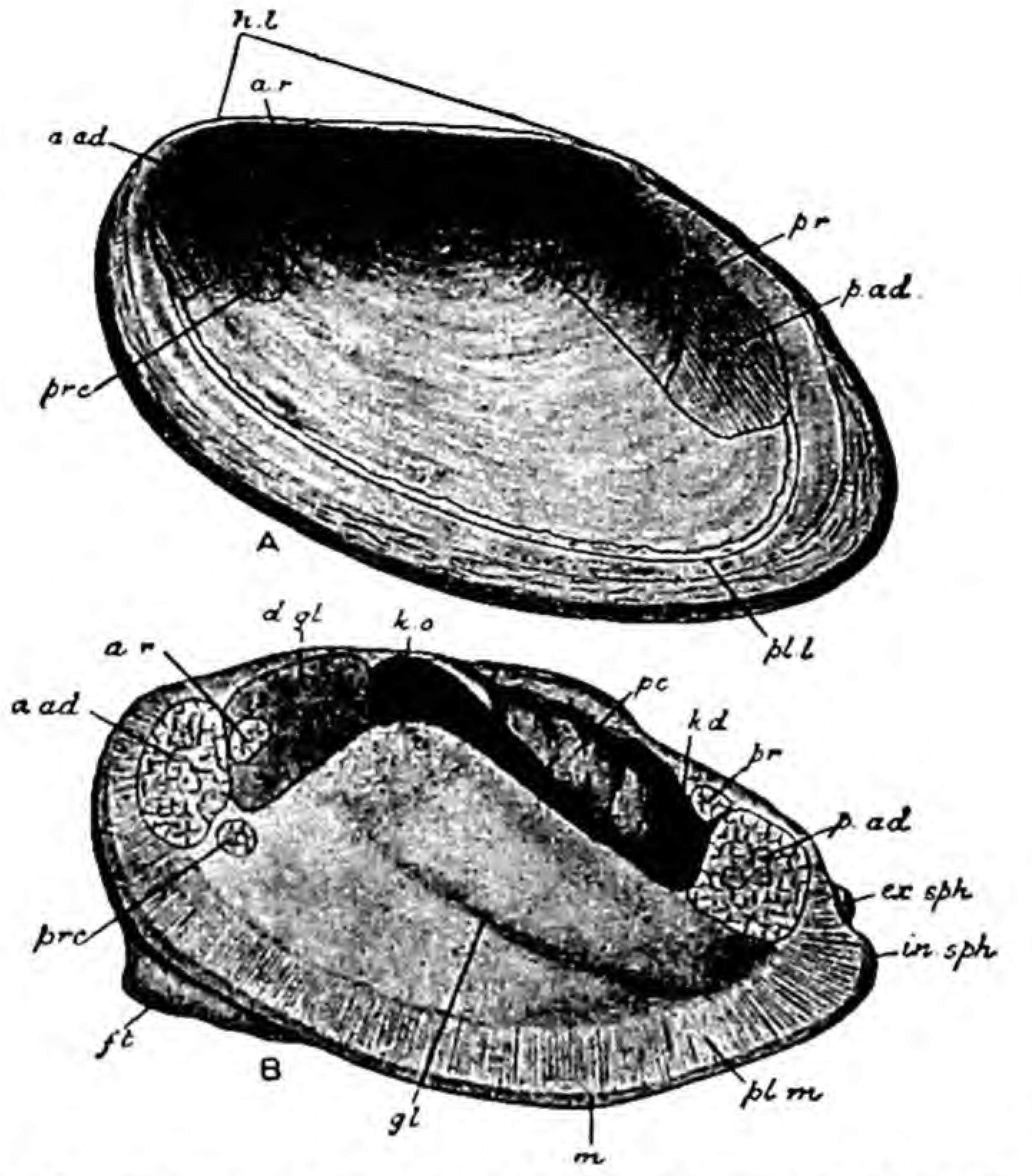


FIG. 580.—**Anodonta cygnea.** *A*, interior of right valve; *B*, the animal removed from the shell. *a. ad.* anterior adductor or its impression; *a. r.* anterior retractor or its impression; *d. gl.* digestive gland, seen through mantle; *ex. sph.* exhalant siphon; *ft.* foot; *gl.* gills, seen through mantle; *h. l.* hinge-line; *in. sph.* inhalant siphon; *kd.* kidney, seen through mantle; *k. o.* Keber's organ, seen through mantle; *m.* mantle; *p. ad.* posterior adductor or its impression; *pc.* pericardium, seen through mantle; *pl. l.* pallial line; *pl. m.* pallial muscles; *p. r.* posterior retractor or its impression; *prc.* protractor or its impression.

The valves are marked externally by a series of concentric lines (Fig. 579) parallel with the free edge or gape, and starting from a swollen knob or elevation, the *umbo* (*um.*), situated towards the anterior edge of the hinge-line. These lines are *lines of growth*. The shell is thickest at the umbo, which represents the part first formed in the young animal, and new layers are deposited under this original portion, as secretions from the mantle. As the animal grows each layer projects beyond its predecessor, and in this way successive outcrops are produced giving rise to the markings in question.

In the region of the umbo the shell is usually more or less eroded by the action of the carbonic acid in the water.

The inner surface of the shell also presents characteristic markings (Fig. 580, *A*). Parallel with the gape and at a short distance from it is a delicate streak (*pl. l.*) caused by the insertion into the shell of muscular fibres from the edge of the mantle: the streak is hence called the *pallial line*. Beneath the anterior end of the hinge the pallial line ends in an oval mark, the *anterior adductor impression* (*a. ad.*), on to which is inserted one of the muscles which close the shell. A similar but larger *posterior adductor impression* (*p. ad.*) lies beneath the posterior end of the hinge. Two smaller markings in close relation with the anterior adductor impression mark the insertion of the *anterior retractor* (*a.r.*), and of the *protractor* (*prc.*) of the foot: one connected with the posterior adductor impression is that of the *posterior retractor* (*p. r.*). From all these impressions faint converging lines can be traced to the umbo: they mark the gradual shifting of the muscles during the growth of the animal.

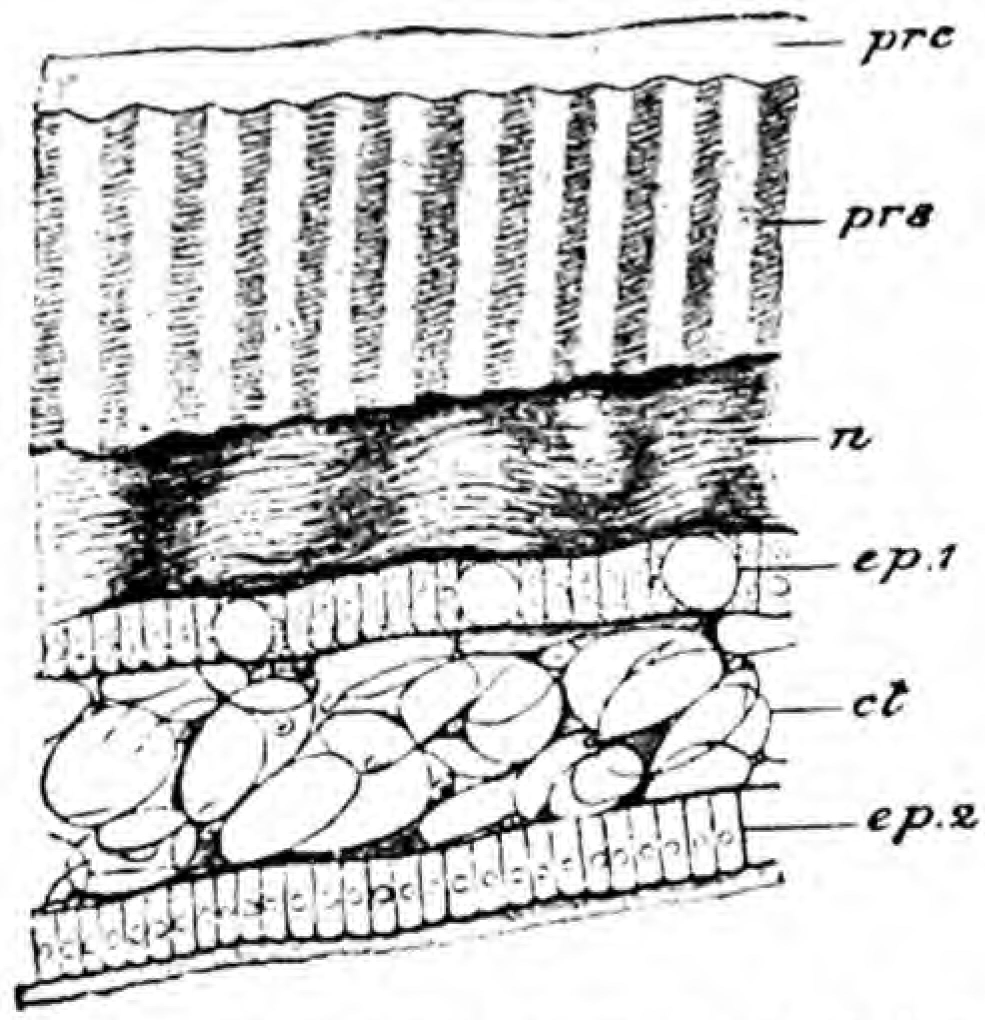


FIG. 581.—Vertical section of shell and mantle of **Anodonta.** *c. t.* connective-tissue layer of mantle; *ep. 1*, its outer epithelium; *ep. 2*, its inner epithelium; *n.* nacreous layer of shell; *prc.* periostracum; *prs.* prismatic layer. (After Claus.)

The shell consists of three layers. Outside is a brown horn-like layer, the *periostracum* (Fig. 581, *prc.*), composed of *conchiolin*, a substance allied in composition to chitin. Beneath this is a *prismatic layer* (*prs.*) formed of minute prisms of calcium carbonate separated by thin layers of conchiolin; and, lastly, forming the internal part of the shell is the *nacre* (*n.*), or "mother-of-pearl," formed of alternate layers of carbonate of lime and conchiolin arranged parallel to the surface. The periostracum and the prismatic layer are secreted from the edge of the mantle only, the pearly layer from the whole of its outer surface. The hinge-ligament is continuous with the periostracum, and is to be looked upon simply as a median uncalcified portion of the shell, which is therefore, in strictness, a single continuous structure.

By the removal of the shell the **body** of the animal (Fig. 580, *B*) is seen to be elongated from before backwards, narrow from side to side, produced on each side into a mantle-lobe (*m.*) and continued ventrally into a keel-like *visceral mass* (Fig. 582, *v.m.*), which passes below and in front into the foot (*ft.*). Thus each valve of the shell is in contact with the dorso-lateral region of the body of its own side together with the corresponding mantle-lobe, and it is from the epithelium (Fig. 581, *ep. 1*) covering these parts that the shell is

formed as a cuticular secretion. The whole space between the two mantle-lobes, containing the gills, visceral mass, and foot, is called the *mantle-cavity*.

A single layer of epithelial cells covers the whole external surface, *i.e.*, the body proper, both surfaces of the mantle, the gills, and foot; that of the gills and of the inner surface of the mantle (Fig. 581, *ep. 2*) is ciliated. Beneath the epidermis come connective and muscular tissue, which occupy nearly the whole of the interior of the body not taken up by the viscera, the cœlome being, as we shall see, much reduced. The **muscles** are all unstriped, and are arranged in distinct bands or sheets, many of them very large and conspicuous. The largest are the *anterior* and *posterior adductors* (Figs. 580 and 582, *a. ad.*,

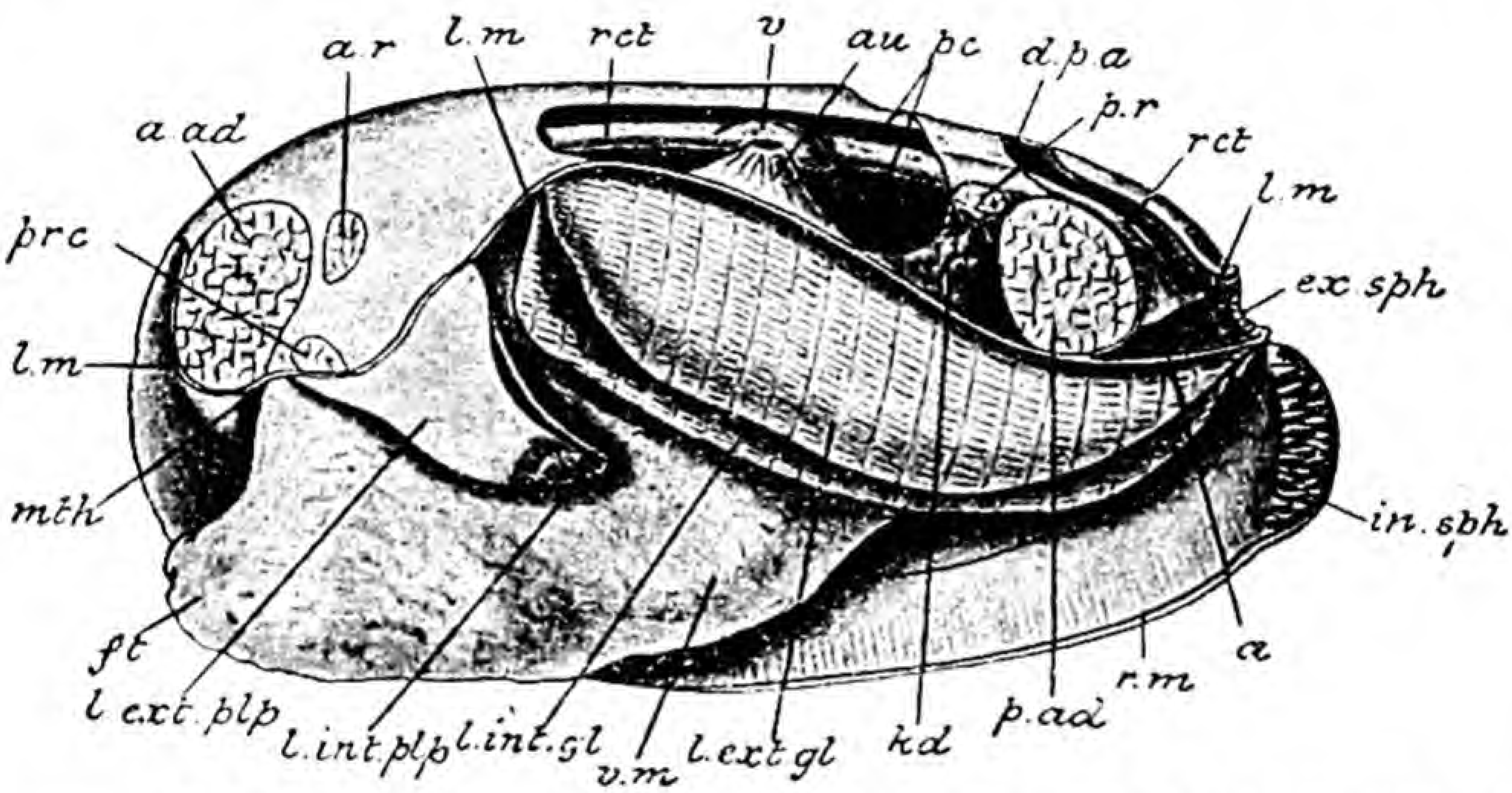


FIG. 582.—**Anodonta cygnea.** The animal with most of the left mantle-lobe removed. *a.* anus; *a. ad.* anterior adductor; *a. r.* anterior retractor; *au.* auricle; *d. p. a.* dorsal pallial aperture; *ex. sph.* exhalant siphon; *ft.* foot; *in. sph.* inhalant siphon; *kd.* kidney; *l. ext. gl.* left external gill-lamina; *l. ext. plp.* left external labial palp; *l. int. gl.* left internal gill-lamina; *l. int. plp.* left internal labial palp; *l. m.* cut edge of left mantle-lobe; *mth.* mouth; *p. ad.* posterior adductor; *pc.* pericardium; *p. r.* posterior retractor; *prc.* protractor; *rct.* rectum; *r. m.* right mantle-lobe; *v.* ventricle; *v. m.* visceral mass.

p. ad.), great cylindrical muscles, passing transversely across the body and inserted at either end on to the valves of the shell, which are approximated by their contraction. Two muscles of much smaller size pass from the foot to the shell, which they serve to draw back; they are the *anterior* (*a. r.*) and *posterior* (*p. r.*) *retractors.* A third muscle (*prc.*), inserted on to the shell, close to the anterior adductor, has its fibres spread fan-wise over the visceral mass, which it serves to compress, thus forcing out the foot and acting as a *protractor* of that organ. The substance of the foot itself consists of a complex mass of fibres, the *intrinsic muscles* of the foot, many of which also act as protractors. Lastly, all along the border of the mantle is a row of delicate *pallial muscles* (Fig. 580, *pl. m.*), which, by their insertion into the shell, give rise to the pallial line already seen.

The **cœlome** is reduced to a single ovoidal chamber, the *pericardium* (Fig. 582, *pc.*), lying in the dorsal region of the body and containing the heart and part of the intestine; it is lined by cœlomic epithelium. In the remainder of the body the space between the ectoderm and the viscera is filled by the muscles and connective-tissue.

Digestive organs.—The *mouth* (Fig. 582, *mth.*) lies in the middle line, just below the anterior adductor. On each side of it are two triangular flaps, the *internal* and *external labial palps* (*l. int. plp.*, *l. ext. plp.*); the external palps unite with one another in front of the mouth, forming an upper lip;

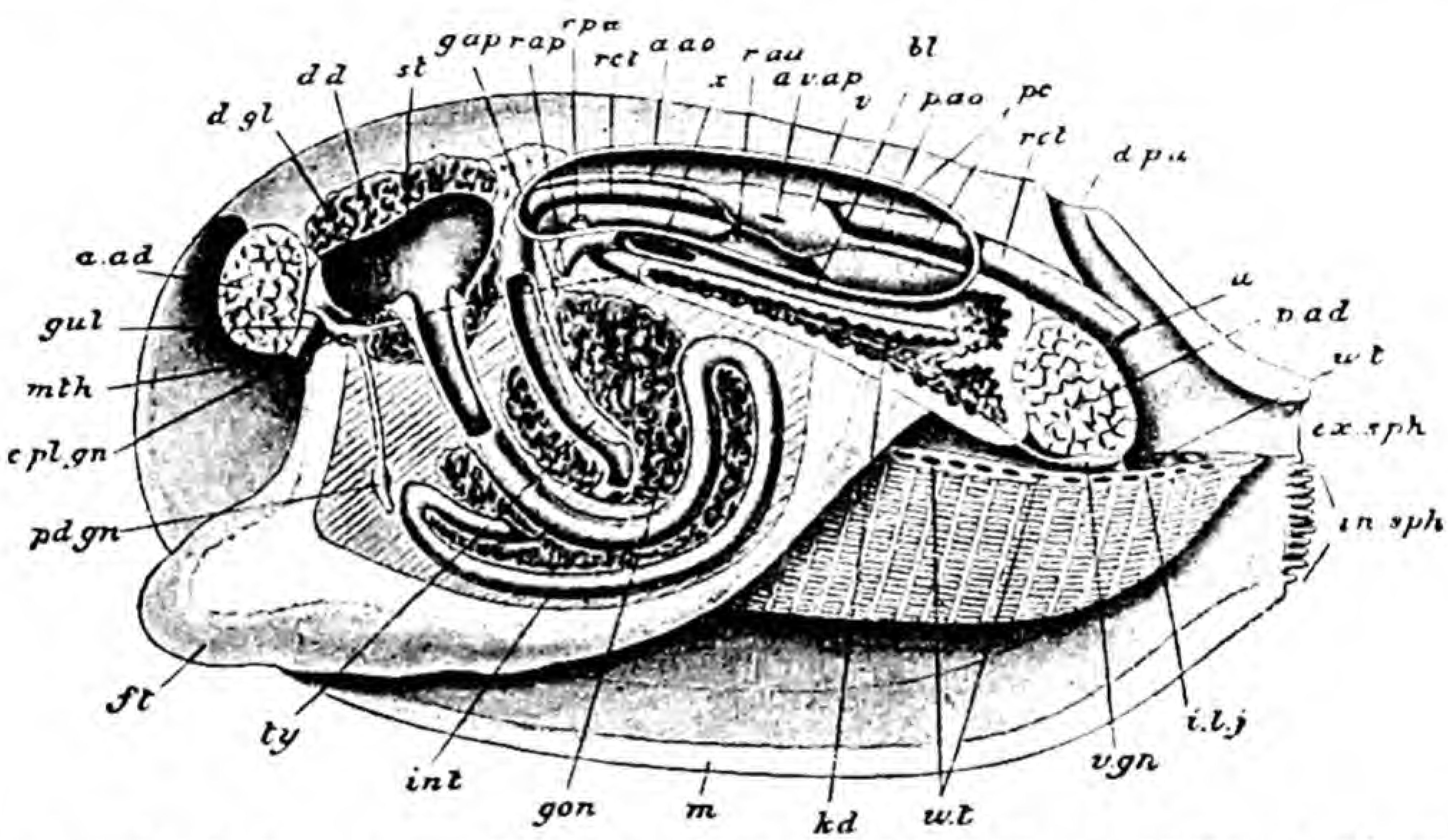


FIG. 583.—**Anodonta cygnea.** Dissection from the left side. *a.* anus; *a. ad.* anterior adductor; *a. ao.* anterior aorta; *a. v. ap.* auriculo-ventricular aperture; *bl.* urinary bladder; *c. pl. gn.* cerebro-pleural ganglion; *d. d.* duct of digestive gland; *d. gl.* digestive gland; *d. p. a.* dorsal pallial aperture; *ex. sph.* exhalant siphon; *ft.* foot; *g. ap.* genital aperture; *gon.* gonad; *gul.* gullet; *i. l. j.* inter-lamellar junction; *in. sph.* inhalant siphon; *int.* intestine; *kd.* kidney; *m.* mantle; *mth.* mouth; *p. ao.* posterior aorta; *p. ad.* posterior adductor; *pc.* pericardium; *pd. gn.* pedal ganglion; *r. ap.* renal aperture; *r. au.* right auricle; *rct.* rectum; *r. p. a.* reno-pericardial aperture; *st.* stomach; *ty.* typhlosole; *v.* ventricle; *v. gn.* visceral ganglion; *w. t.* water tubes; *x.* aperture between right and left bladders.

the internal palps are similarly united behind the mouth, forming a lower lip; both are ciliated externally. The mouth leads by a short *gullet* (Fig. 583, *gul.*) into a large *stomach* (*st.*), which receives the ducts (*d.d.*) of a pair of irregular, dark-brown *digestive glands* (*d. gl.*). The *intestine* (*int.*) is given off from the posterior end of the stomach, descends into the visceral mass, where it is coiled upon itself, then ascends parallel to its first portion, turns sharply backwards, and proceeds, as the *rectum* (*rct.*), through the pericardium—where it traverses the ventrical of the heart—and above the posterior adductor, finally discharging by the *anus* (*a.*) into the exhalant siphon, or cloaca. The wall of the rectum is produced into a longitudinal ridge, or *typhlosole* (*ty.*), like that of the Earthworm, and two similar ridges begin in the stomach and

are continued into the first portion of the intestine. The stomach contains, under certain conditions, a gelatinous rod, the *crystalline style*, which plays an important part in the process of digestion.

On each side is a single **gill** or **ctenidium** composed of two plates or *laminæ*, an inner and an outer. We have thus right outer and inner gill-laminæ, and left outer and inner gill-laminæ (Fig. 582, *l. ext. gl.*, *l. int. gl.*). Seen from the

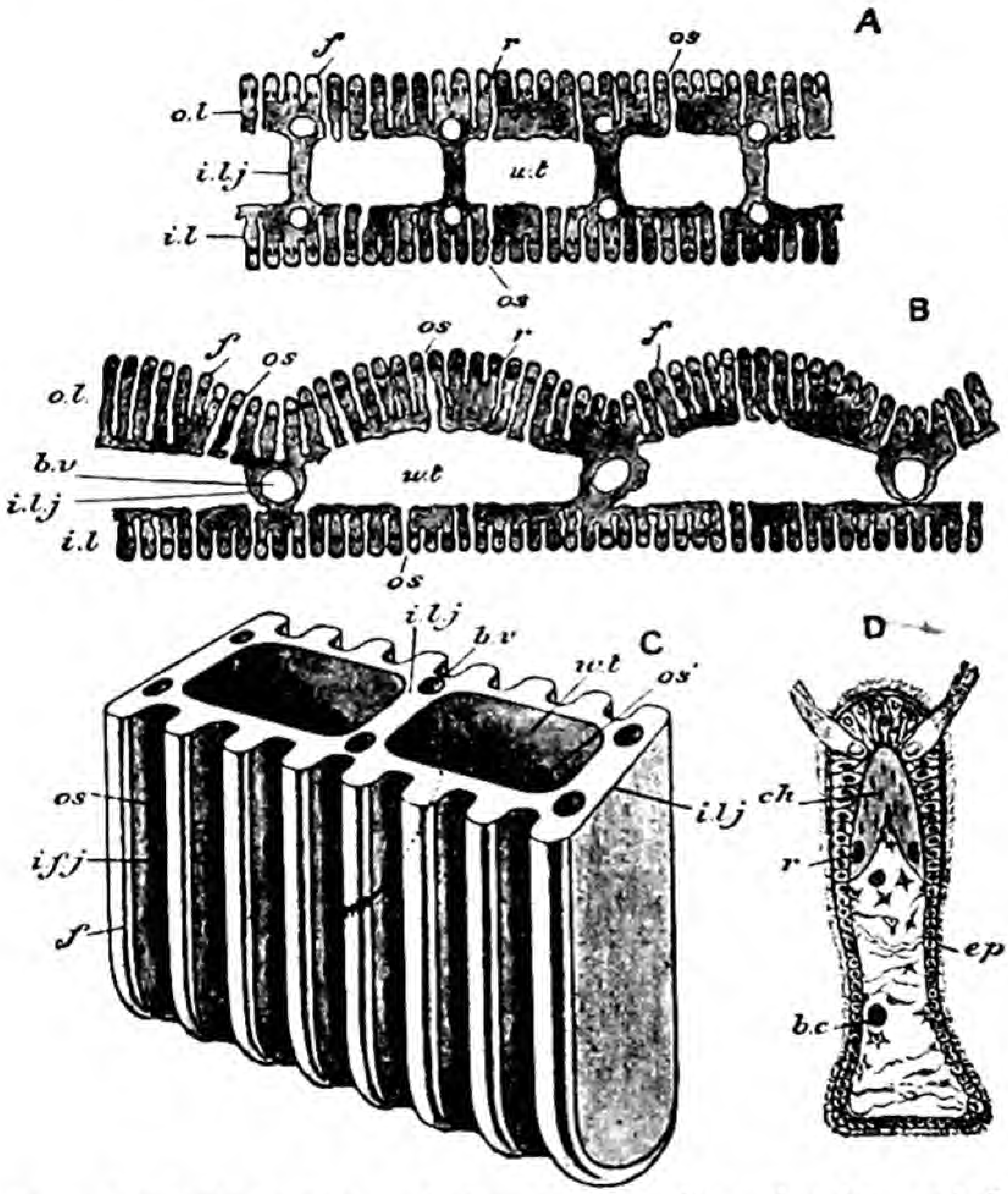


FIG. 584.—**Anodonta cygnea.** *A*, transverse section of outer, and *B*, of inner gill-lamina; *C*, diagram of gill-structure; *D*, transverse section of gill filament. *b. c.* blood-corpuscle; *b. v.* blood-vessels; *ch.* chitin; *f.* branchial filaments; *ep.* epithelium; *i. f. j.* inter-filamentar junction; *i. l.* inner lamella; *i. l. j.* inter-lamellar junction; *o. l.* outer lamella; *os.* external ostium; *os'* internal ostium; *r*, chitinous rods; *w. t.* water-tubes. (*A*, *B*, and *D* after Peck.)

surface, each lamina presents a delicate double striation, being marked by faint lines running parallel with, and by more pronounced lines running at right angles to, the long axis of the organ. Moreover, each lamina is double, being formed of two similar plates, the *inner* and *outer lamellæ*, united with one another along the anterior, ventral, and posterior edges of the lamina, but free dorsally. The lamina has thus the form of a long and extremely narrow bag open above (Figs. 583, 584, and 585): its cavity is subdivided by

vertical bars of tissue, the *inter-lamellar junctions* (*i. l. j.*), which extend between the two lamellæ, and divide the intervening space into distinct compartments or *water-tubes* (*w.t.*), closed ventrally, but freely open along the dorsal edge of the gill. The vertical striation of the laminæ is due to the fact that

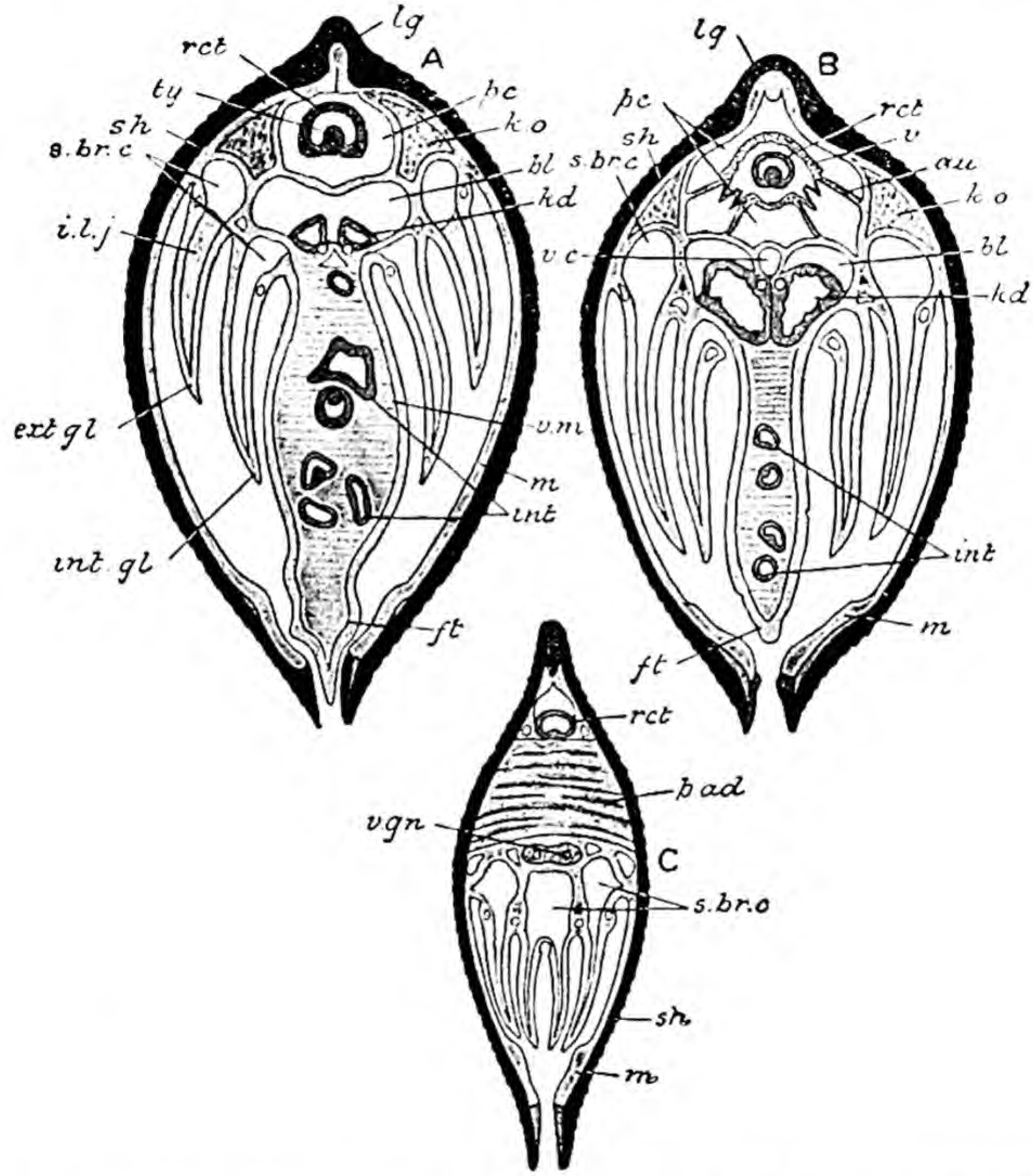


FIG. 585.—**Anodonta cygnea.** Three transverse sections, *A*, *B*, *C*, *au.* auricle; *bl.* urinary bladder; *ext. gl.* external gill-lamina; *ft.* foot; *i. l. j.* inter-lamellar junction; *int.* intestine; *int. gl.* internal gill-lamina; *kd.* kidney; *k. o.* Keber's organ; *lg.* ligament; *m.* mantle; *p. ad.* posterior adductor; *pc.* pericardium; *rct.* rectum; *s. br. c.* supra-branchial chamber; *sh.* shell; *ty.* typhlosole; *v.* ventricle; *vc.* vena cava; *v. gn.* visceral ganglion. (After Howes, slightly altered.)

each lamella is made up of a number of close-set *gill-filaments* (*f.*): the longitudinal striation to the circumstance that these filaments are connected by horizontal bars, the *inter-filamentar junctions* (*i. f. j.*). At the thin free or ventral edge of the lamina the filaments of the two lamellæ are continuous with one another, so that each lamina has actually a single set of V-shaped

filaments, the outer limbs of which go to form the outer lamella, their inner limbs the inner lamella. Between the filaments, and bounded above and below by the inter-filamentar junctions, are minute apertures, or *ostia* (*os.*), which lead from the mantle-cavity through a more or less irregular series of cavities into the interior of the water-tubes. The filaments themselves are supported by chitinous rods (*r.*), and are covered with ciliated epithelium, the large cilia (Fig. 584, *D*) of which produce a current running from the exterior through the ostia into the water-tubes, and finally escaping by the wide dorsal apertures of the latter. The whole organ is traversed by blood-vessels (*b. v.*).

The mode of attachment of the gills presents certain features of importance. The outer lamella of the outer lamina is attached along its whole length to the mantle (Fig. 585): the inner lamella of the outer and the outer lamella of the inner lamina are attached together to the sides of the visceral mass a little below the origin of the mantle: the inner lamella of the inner lamina is also attached to the visceral mass in front (*A*), but is free farther back (*B*). The gills are longer than the visceral mass, and project behind it, below the posterior adductor (*C*), as far as the posterior edge of the mantle: in this region the inner lamellæ of the right and left inner laminæ are united with one another, and the dorsal edges of all four laminæ constitute a horizontal partition between the pallial cavity below and the exhalant chamber or cloaca above. Owing to this arrangement it will be seen that the water-tubes all open dorsally into a *supra-branchial chamber* (*s. br. c.*). continuous posteriorly with the cloaca and thus opening on the exterior by the exhalant siphon.

The physiological importance of the gills will now be obvious. By the action of their cilia a current is produced which sets in through the inhalant siphon into the pallial cavity, through the ostia into the water-tubes, into the supra-branchial chamber, and out at the exhalant siphon. The in-going current carries with it not only oxygen for the aëration of the blood, but also Diatoms, Infusoria and other microscopic organisms, which are swept into the mouth by the cilia covering the labial palps. The out-going current carries with it the various products of excretion and the fæces passed into the cloaca. The action of the gills in producing the food-current is of more importance than their respiratory function, which they share with the mantle.

The **excretory organs** are the *kidneys* or *urocœles* (portions of the true cœlome), situated one on each side of the body just below the pericardium. Each consists of two parts, a brown spongy *glandular portion* or *kidney* (Fig. 583, *kd.*), and a thin-walled non-glandular part or *urinary bladder* (*bl.*), which communicates with its fellow anteriorly by a large oval aperture (*x*). The two parts lie parallel to one another, the bladder being placed dorsally and immediately below the floor of the pericardium: they communicate with one another posteriorly, while in front each glandular part opens into

the pericardium (*r. p. ap.*), and the bladder on to the exterior by a minute aperture (*r. ap.*), situated between the inner lamina of the gill and the visceral mass. Thus the whole organ, often called, after its discoverer, the *organ of Bojanus*, is simply a tube bent upon itself, opening at one end into the cœlome, and at the other on the external surface of the body : it has thus the normal relations of a cœlomoduct and is of cœlomic derivation. The epithelium of the bladder is ciliated, and produces an outward current.

An excretory function is also discharged by a large glandular mass of reddish-brown colour, called the *pericardial gland* or *Keber's organ* (Fig. 585,

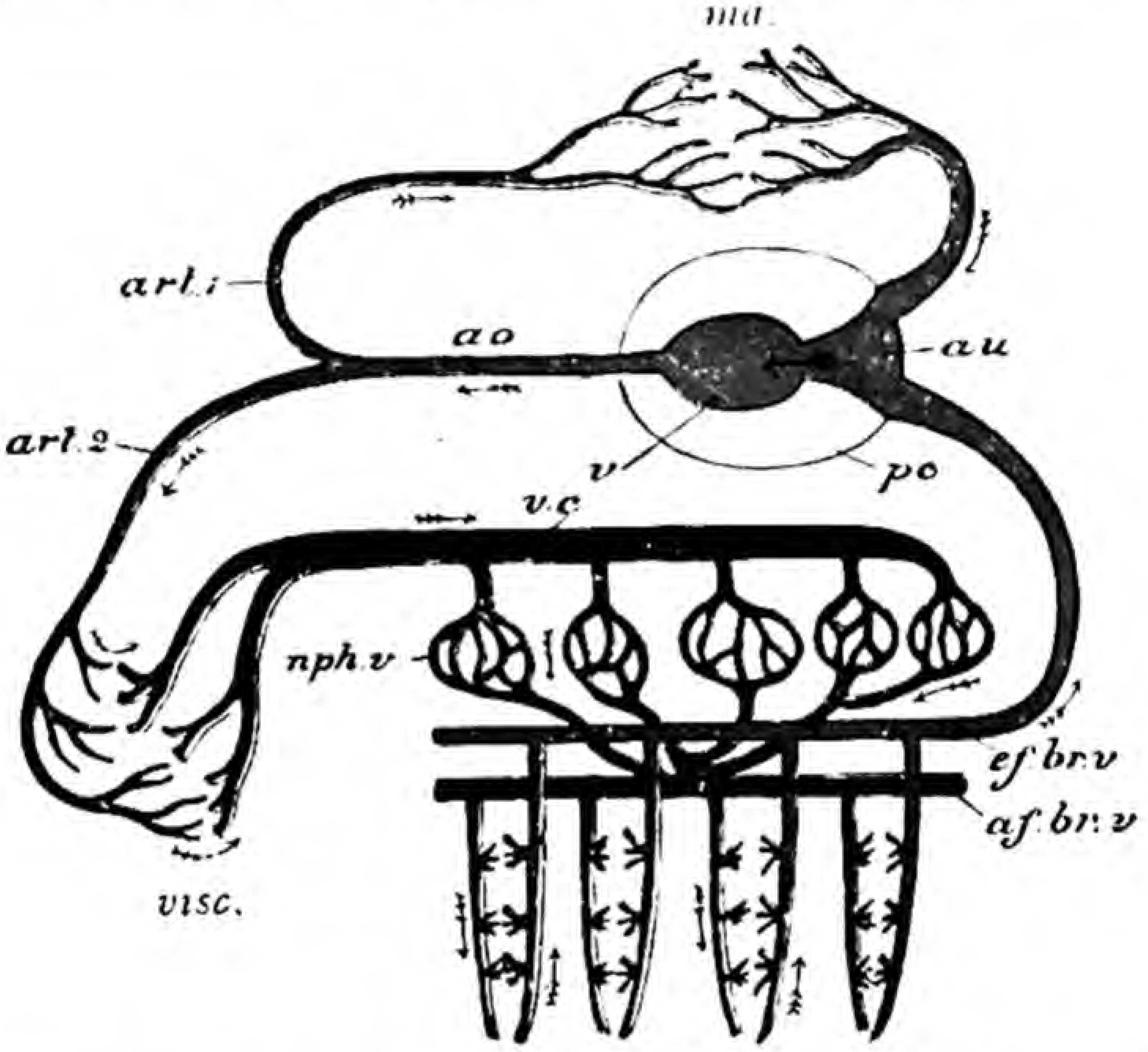


FIG. 586.—Simplified diagram of the circulatory system of **Anodonta.** Vessels containing mainly aërated blood red, non-aërated blue. *af. br. v.* afferent branchial veins ; *ao.* aorta ; *art. 1*, artery to mantle ; *art. 2*, artery to body generally ; *au.* auricle ; *ef. br. v.* efferent branchial veins ; *ma.* mantle ; *nph. v.* renal veins ; *pc.* pericardium ; *v.* ventricle ; *v. c.* vena cava ; *visc.* viscera. The arrows show the direction of the current.

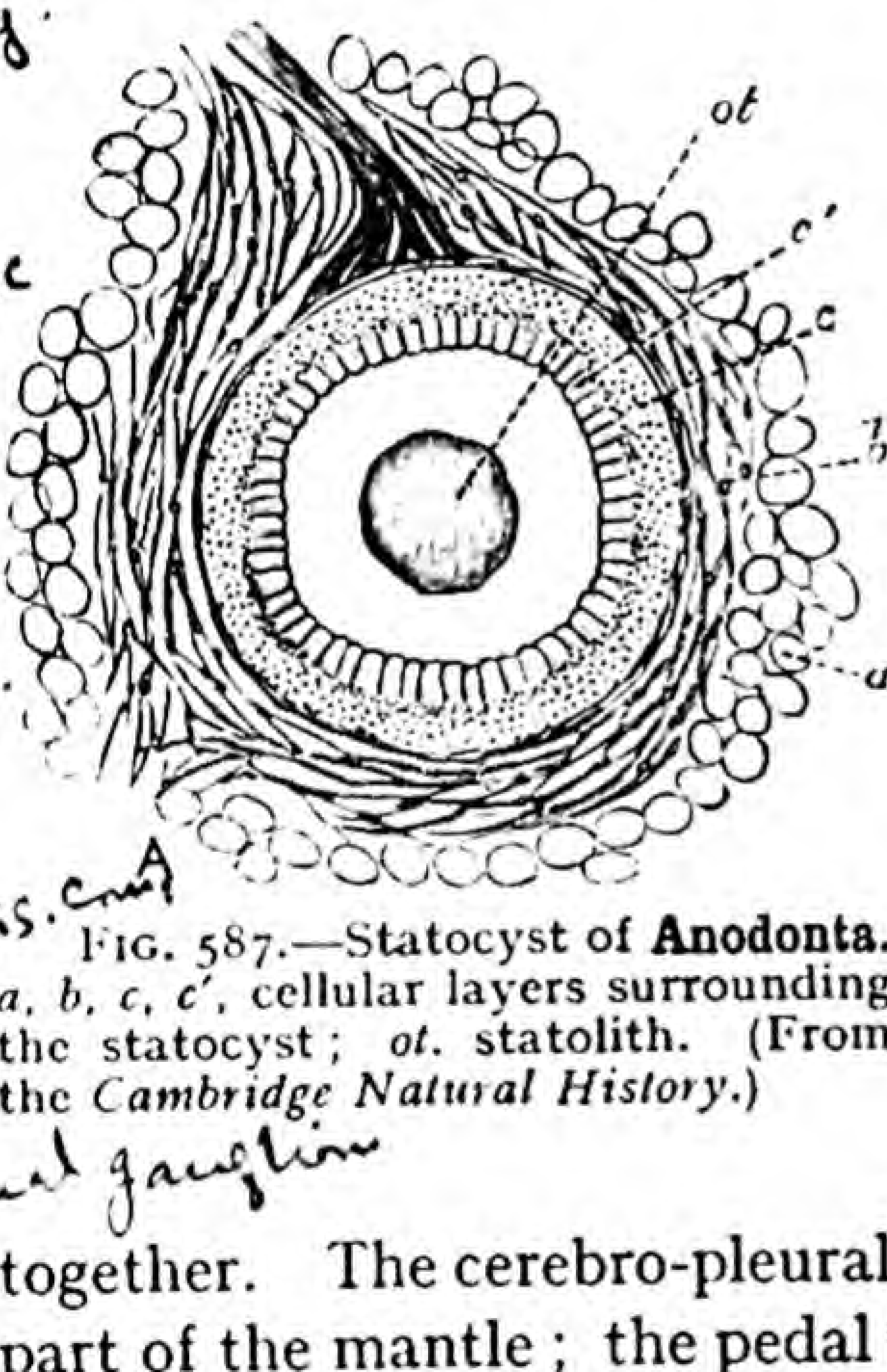
B, k.o.). It lies in the anterior region of the body just in front of the pericardium, into which it discharges.

The **circulatory system** is well developed. The *heart* lies in the pericardium and consists of a single *ventricle* (Figs. 583, 585, and 586, *v.*) and of right and left *auricles* (*au.*). The ventricle is a muscular chamber which has the peculiarity of surrounding the rectum (Figs. 583 and 585, *B*) : the auricles are thin-walled chambers communicating with the ventricle by valvular apertures opening towards the latter. From each end of the ventricle an artery is given off, the *anterior aorta* (Fig. 583, *a. ao.*) passing above, the *posterior aorta* (*p. ao.*) below the rectum. From the aortæ the blood passes into arteries (Fig. 586, *art. 1, art. 2*) which ramify all over the body, finally forming an extensive

network of vessels, many of which are devoid of proper walls and have therefore the nature of sinuses. The returning blood passes into a large longitudinal vein, the *vena cava* (*v. c.*), placed between the kidneys, whence it is taken to the kidneys themselves (*nph. v.*), thence by *afferent branchial veins* (*af. br. v.*) to the gills, and is finally returned by *efferent branchial veins* (*ef. br. v.*) to the auricles. In a short-circuit not shown in Fig. 586, blood is conducted from the vena cava straight to the auricles without passing through kidney and gills. The heart, therefore, receives a certain proportion of non-aërated blood. The mantle has a very extensive blood supply, and, as mentioned above, probably acts as an important respiratory organ: its blood (*art. 1*) is returned directly to the auricles without passing through either the kidneys or the gills. The blood is colourless and contains leucocytes.

Nervous system.—On each side of the gullet is a small *cerebro-pleural ganglion* (Fig. 583, *c. pl. gn.*) united with its fellow of the opposite side by a nerve-cord, the *cerebral commissure*, passing above the gullet. Each cerebro-pleural ganglion also gives off a cord, the *cerebro-pedal connective*, which passes downwards and backwards to a *pedal ganglion* (*pd. gn.*) situated at the junction of the visceral mass with the foot: the two pedal ganglia are so closely united as to form a single bilobed mass. From each cerebro-pleural ganglion there further proceeds a long *cerebro-visceral connective* which passes directly backwards, through the kidney, and ends in a *visceral ganglion* (*v. gn.*) placed on the ventral side of the posterior adductor muscle. The visceral, like the pedal ganglia, are fused together. The cerebro-pleural ganglia supply the labial palps and the anterior part of the mantle; the pedal the foot and its muscles; the visceral, the enteric canal, heart, gills, and posterior portion of the mantle.

c.p.g.
c.p.c
p.g.



c.vis.cnt
FIG. 587.—Statocyst of **Anodonta.** *a, b, c, c'*, cellular layers surrounding the statocyst; *ot.* statolith. (From the *Cambridge Natural History*.)
visceral ganglion

Sense-organs are poorly developed, as might be expected in an animal of such sedentary habits. In connection with each visceral ganglion is a patch of sensory epithelium forming the *osphradium*, an organ of the chemical sense the function of which is to test the purity of the water entering by the respiratory current. Close to each pedal ganglion a minute *statocyst* (Fig. 587) is sometimes found, the nerve of which is said to spring from the cerebro-pedal connective, being probably derived from the cerebral ganglion. Sensory cells—probably tactile—also occur round the edge of the mantle, and especially on the fimbriæ of the inhalant siphon.

Reproductive organs.—The sexes are separate. The gonads (Fig. 583,

gon.) are large, paired, racemose glands, occupying a considerable portion of the visceral mass amongst the coils of the intestine: the testis is white, the ovary reddish. The gonad of each side has a short duct which opens (*g. ap.*) on the surface of the visceral mass just in front of the renal aperture.

In the breeding season the eggs, extruded from the genital aperture, pass into the supra-branchial chamber and so to the cloaca. There, in all probability, they are fertilized by sperms introduced with the respiratory current. The fertilized ova are then passed into the cavities of the outer gill-laminæ, which they distend enormously. Thus the outer gill-laminæ act as brood-pouches, and in them the embryo develops into the peculiar larval form presently to be described.

Development.—Cleavage is complete, but unequal. A gastrula is formed by the invagination of the macromeres into the micromeres, but the archenteron (Fig. 588, *ent.*) thus formed is quite small and insignificant, and has no physiological importance until a late period of larval life. Certain of the cells of the gastrula are budded off into the blastocœle, where they accumulate and form the mesoderm (*mes.*). At about the same time a deep invagination (*sd.*) is formed, which might easily be mistaken for the archenteron, but is really a very characteristic molluscan organ, the *shell-gland*: it marks the dorsal surface of the embryo. The posterior end is distinguished by a tuft of long cilia.

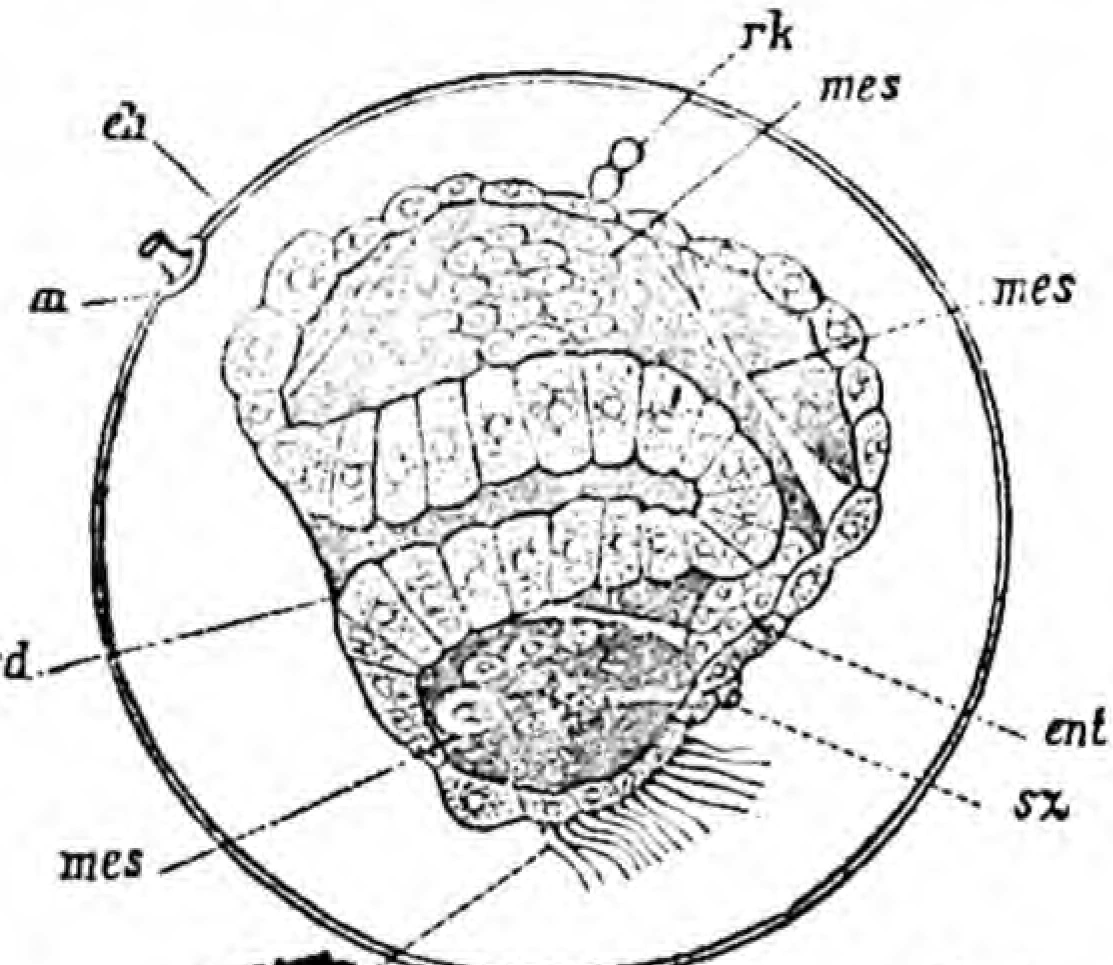


FIG. [illegible] y embryo of **Anodonta.** *ch.* vitellin[illegible] c; *ent.* archenteron; *m.* microp[illegible] mesoderm; *rk*, polar cells; *sd*, she[illegible], lateral cells; *w*, cilia. (From Korsc[illegible]eider's *Embryology*.)

The shell-gland becomes converted into a plate of long, cylindrical cells (Fig. 589, *sd.*), from which an *unpaired* shell (*s.*) is secreted. This is replaced before long by a bivalved shell of triangular form, its ventral angles produced into incurved hooks beset with spines (Fig. 590, *sh*). At the same time the body of the larva, which has hitherto been an undivided mass projecting between the two valves of the shell, becomes cleft from below upwards, and thus divided into a single dorsally-placed body proper, and paired—right and left—mantle-lobes. Upon the latter peculiar brush-like sense-organs make their appearance, and on the ventral surface of the body is formed a glandular pouch, which secretes a long thread, the *provisional byssus* (*f.*). The mesoderm cells give rise to a single immense adductor muscle (*sm.*), the fibres of which extend from valve to valve.

The larva is now called a *glochidium*: it remains in the brood-pouch, nourished by a secretion from the walls of the latter, and entangled with its fellows by means of the byssus. At this stage the outer gill-lamina appears as if stuffed full of closely aggregated sand-grains. Before long the larvæ

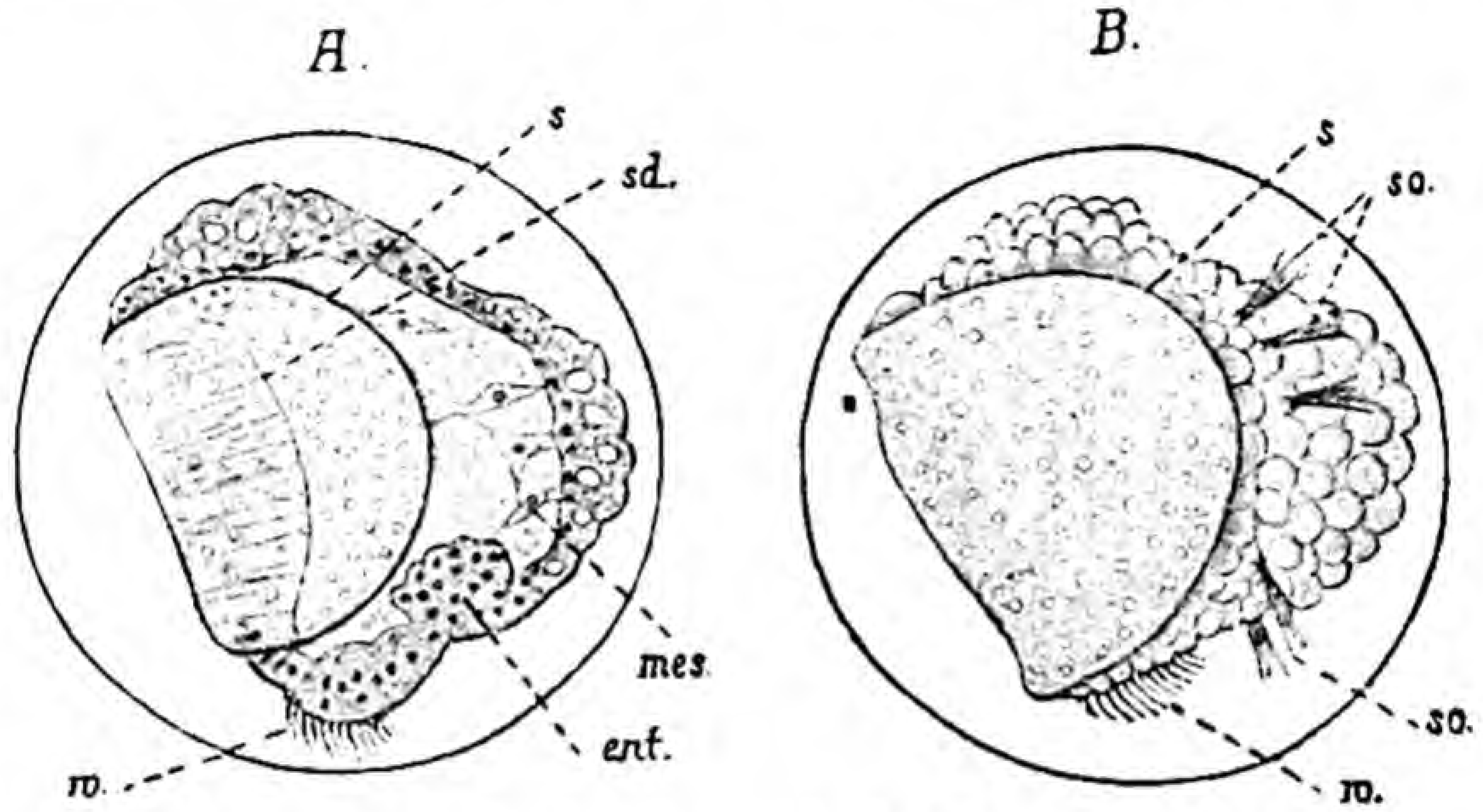


FIG. 589.—Two later stages in the development of **Anodonta.** *ent.* archenteron; *mes.* mesoderm; *s.* shell; *sd.* shell-gland; *so.* sense-organs; *w.* cilia. (From Korschelt and Heider's *Embryology*.)

are ejected through the exhalant siphon, and if they happen to come in contact with a passing Stickleback or other fresh-water fish, fix themselves on some part of its body by means of the hooked valves. The glochidia of Unio usually attach themselves to the gills, those of Anodonta to the skin or the

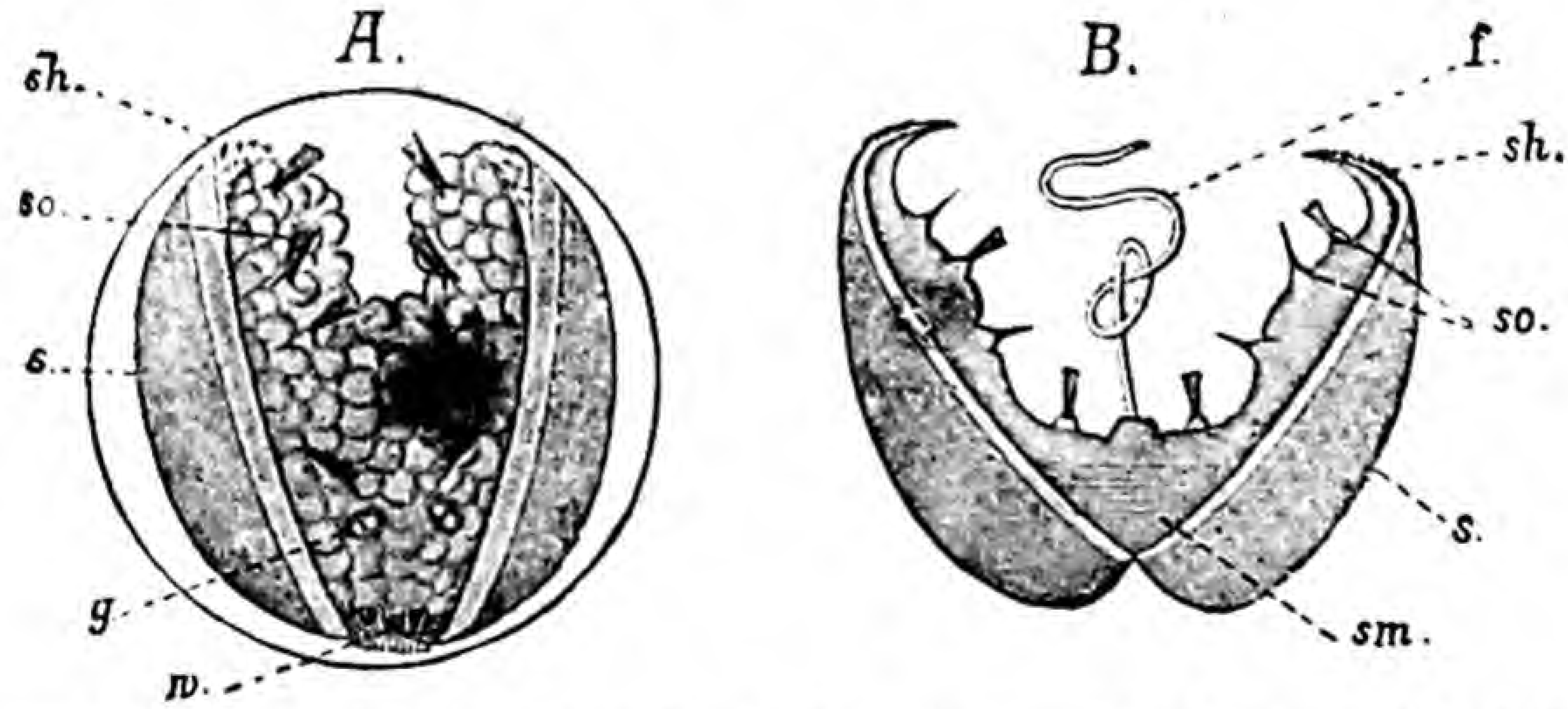


FIG. 590.—*A*, advanced embryo of **Anodonta.** *B*, free glochidium. *f*, provisional byssus; *g*. lateral pits; *s*. shell; *sh*. hooks; *sm*. adductor muscle; *so*. sense-organs; *w*. cilia. (From Korschelt and Heider's *Embryology*.)

fins. In this position they become encysted by an overgrowth of the skin or mucous membrane of the host, and are nourished by its juices absorbed through processes of the mantle. They thus lead a truly ectoparasitic existence for about ten weeks.

While in this condition, a metamorphosis takes place. The provisional byssus and sense-organs disappear (Fig. 591), and immediately posterior to the former an invagination, the *stomodæum* (*m.*), is formed, and soon communicates with the archenteron. The posterior end of this cavity is in close contact with the ectoderm, so that the anus is formed by a simple process of rupture, and without the development of a proctodæum. The foot (*fu.*)

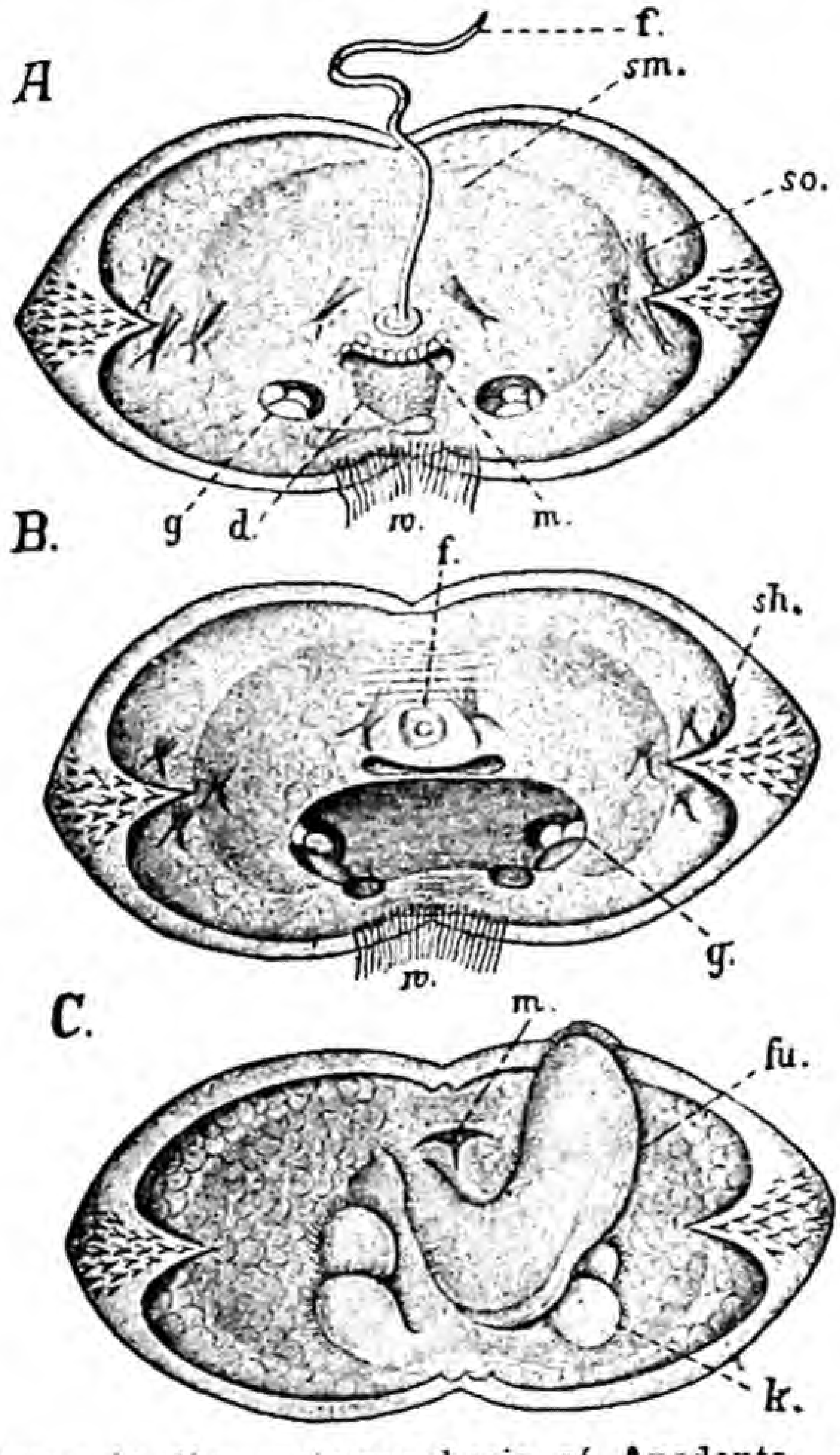


FIG. 591.—Three stages in the metamorphosis of **Anodonta.** *d.* enteric canal; *f.* provisional byssus; *fu.* foot; *g.* lateral pits; *k.* rudiments of gills; *m.* mouth; *sh.* shell; *sm.* adductor muscle; *so.* sense-organs; *w.* cilia. (From Korschelt and Heider's *Embryology*.)

arises as a median ventral elevation behind the mouth, and on each side of it two papillæ (*k.*) appear, the rudiments of the gills. The larva is now fitted for free existence; it drops from its host, and gradually assumes the adult form and mode of life.

2. Distinctive Characters and Classification.

The Bivalvia are bilaterally symmetrical, compressed Molluscs, in which the mantle consists of paired right and left lobes, secreting a bivalved calcareous shell.

There is no distinct head. The ventral region of the body is differentiated into a muscular foot, which is usually ploughshare- or tongue-shaped ; in some cases there is a byssus-gland *posterior to the foot, which secretes a mass of horny fibres, the* byssus, *by which the animal may be permanently attached. There are two gills or* ctenidia, *one on each side : the chief function of the gills is the production of a respiratory and food-carrying current of water. The body is covered by a one-layered epidermis, which is ciliated on the gills and on the inner surface of the mantle. The muscular system is well-developed, the largest muscles being either one or two adductors, which close the shell, and several bands connected with the foot and the byssus ; the muscles are usually unstriped. The cœlome is reduced to a dorsally-placed pericardium. The mouth is bounded by two pairs of flat, triangular tentacles or labial palps, the cilia of which serve to carry food-particles to the mouth : the enteric canal is coiled, and is formed mainly from the mesenteron : there are large paired digestive glands : the rectum passes through the pericardium, usually perforates the ventricle, and ends above the posterior adductor. The heart is contained within the pericardium, and consists of a median ventricle and of right and left auricles : the blood, which frequently contains hæmocyanin, sometimes hæmoglobin, is taken from the ventricle to the body by one or two aortæ, and is returned partly directly, partly by way of the renal organs and gills, to the auricles. The renal organs are a single pair of cœlomic kidneys, which usually open at one end into the pericardium, at the other on the exterior. The nervous system consists typically of four pairs of ganglia called respectively cerebral, pleural, pedal, and visceral : the cerebral and pleural of each side are usually fused into a single cerebro-pleural ganglion. The chief sense-organs are statocysts and osphradia or water-testing organs. The sexes are separate or united : there are no accessory organs of reproduction. Development is accompanied by a metamorphosis, which usually includes a trochophore stage.*

The classification of the Bivalvia is as follows :—

ORDER 1.—PROTOBRANCHIATA.

Bivalvia in which the gills take the form of a single pair of plume-like organs or ctenidia, each with two rows of flattened gill-filaments. The foot is not compressed, but has a flattened ventral surface or sole upon which the animal creeps. There are two adductor muscles.

This group includes *Nucula* (Fig. 603), *Yoldia*, *Leda*, and *Solenomya*.

ORDER 2.—FILIBRANCHIATA.

Bivalvia in which there is a pair of plate-like gills formed of distinct V-shaped filaments : interfilamentar junctions are either absent or formed by groups of interlocking cilia : interlamellar junctions are either absent or non-vascular. As a rule there are two adductor muscles, but the anterior may be greatly reduced or absent.

Including the Noah's ark shell (*Arca*), *Modiola*, Sea-mussel (*Mytilus*, Fig. 602), *Amusium*, *Anomia*, *Trigonia*, etc.

ORDER 3.—PSEUDO-LAMELLIBRANCHIATA.

Bivalvia in which the gills are plaited so as to present vertical folds: the interfilamentar junctions may be ciliary or vascular: the interlamellar junctions vascular or non-vascular. There is a single large (posterior) adductor muscle. The shell is frequently inequivalve.

Including the Scallop (*Pecten*, Fig. 592), Oyster (*Ostrea*), Pearl Oyster (*Meleagrina*), *Lima*, *Vulsella*, *Pinna*, etc.

ORDER 4.—EULAMELLIBRANCHIATA.

Bivalvia in which the gill-filaments are united by vascular interfilamentar and interlamellar junctions, firm, basket-like gills being the result: the gills may be smooth or plaited. There are two equal-sized adductor muscles.

Sub-order a.—Integripalliata.

Eulamellibranchiata in which the siphons are small or absent and the pallial line on the shell is entire.

Including the fresh-water Mussels (*Anodonta* (Fig. 579), *Unio*, and *Sphærium*).

Sub-order b.—Sinupalliata.

Eulamellibranchiata in which the siphons are of considerable size, and the pallial line is inflected to form a sinus.

Including the Cockle (*Cardium*, Fig. 594), *Venus*, *Scrobicularia*, *Donax*, *Solenocurtus*, *Mya*, *Pholas*, *Teredo* (Ship-worm, Fig. 600), *Brechites*, etc.

ORDER 5.—SEPTIBRANCHIATA.

Bivalvia in which the gills are reduced to a horizontal muscular partition. There are two adductor muscles.

Including *Poromya* (Fig. 606), *Cuspidaria*, etc.

3. GENERAL ORGANIZATION.

The most important variations in structure in the present class are connected with modifications of the gills, the foot, the muscular system, and the siphons. With the structure of the muscles and of the siphons are correlated important variations in the shell which are of great systematic value, especially in cases where, as with fossils, the shell is the only part available for examination.

In all the Protobranchiata, some of the Filibranchiata, such as *Arca*, and all the Eulamellibranchiata and Septibranchiata, there are two almost equal-sized **adductor muscles,** as in Anodonta. In many Filibranchiata, such as the

common Sea-mussel (*Mytilus edulis*), the anterior adductor becomes greatly reduced and the posterior correspondingly enlarged; and in another species of the same genus (*M. latus*) the anterior adductor has completely atrophied, the function of closing the shell being performed by the great posterior adductor alone. In Anomia and in the Pseudolamellibranchiata there is a single immense adductor (Fig. 592, X, XI) placed nearly in the middle of the greatly shortened body, and known to represent the posterior adductor—both from the fact that the rectum passes over it, and from the circumstance that, in the embryo

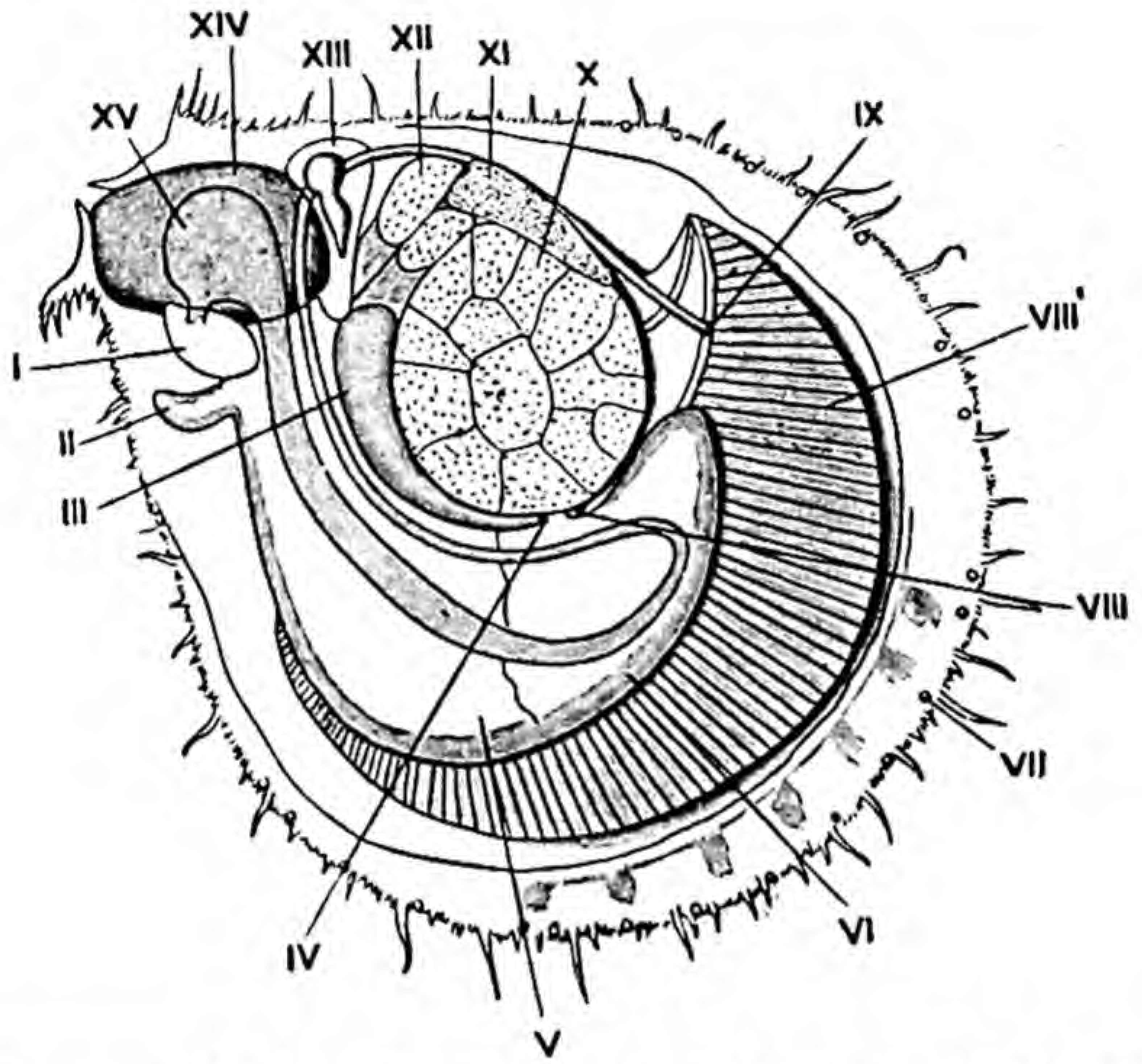


FIG. 592.—Anatomy of **Pecten.** I, palpi; II, foot; III, aperture of gonad into kidney; IV, external renal aperture; V, male, and VI, female portion of gonad; VII, pallial eye; VIII, visceral ganglion; VIII′, gill; IX, anus; X, striated portion of adductor; XI, smooth portion; XII, retractor of foot; XIII, heart; XIV, liver; XV, stomach. (From Pelseneer's *Mollusques.*)

Oyster, two adductors are present, the anterior of which atrophies, while the posterior enlarges to form the single muscle of the adult.

These peculiarities in the muscular system bear their mark upon the **shell,** in which impressions corresponding to the adductors are clearly marked on the inner surface (Fig. 593). The whole class is, in fact, frequently classified on this basis, species with equal-sized adductors (Protobranchiata, some Filibranchiata, and all Eulamellibranchiata and Septibranchiata) being called *Isomyaria* (*A*), those with a large posterior and a reduced anterior adductor (most Filibranchiata) *Heteromyaria* (*B*), and those with large centrally placed posterior and no anterior adductor (Pseudolamellibranchiata and Anomia among the Filibranchiata) *Monomyaria* (*C*).

In many forms, such as Nucula (Fig. 603), Ostrea, etc., the right and left mantle-lobes are quite free from each other, so that there are no siphons. In

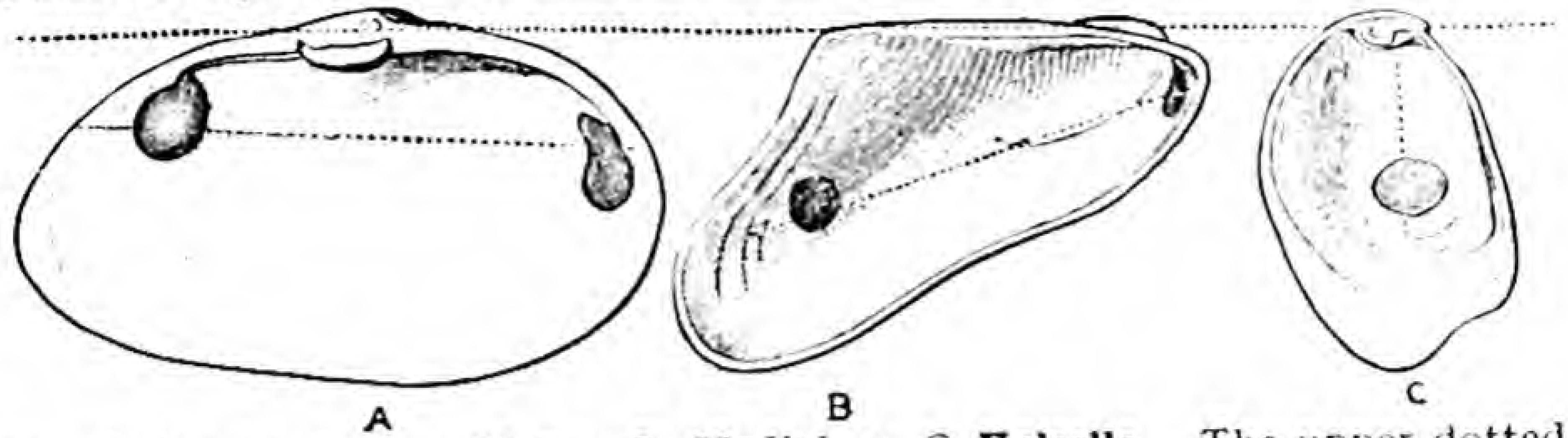


FIG. 593.—Left valves of *A*, **Mya** ; *B*, **Modiola** ; *C*, **Vulsella.** The upper dotted line passes through the hinge-lines, the lower connects the anterior and posterior adductor muscles. (From the *Cambridge Natural History*.)

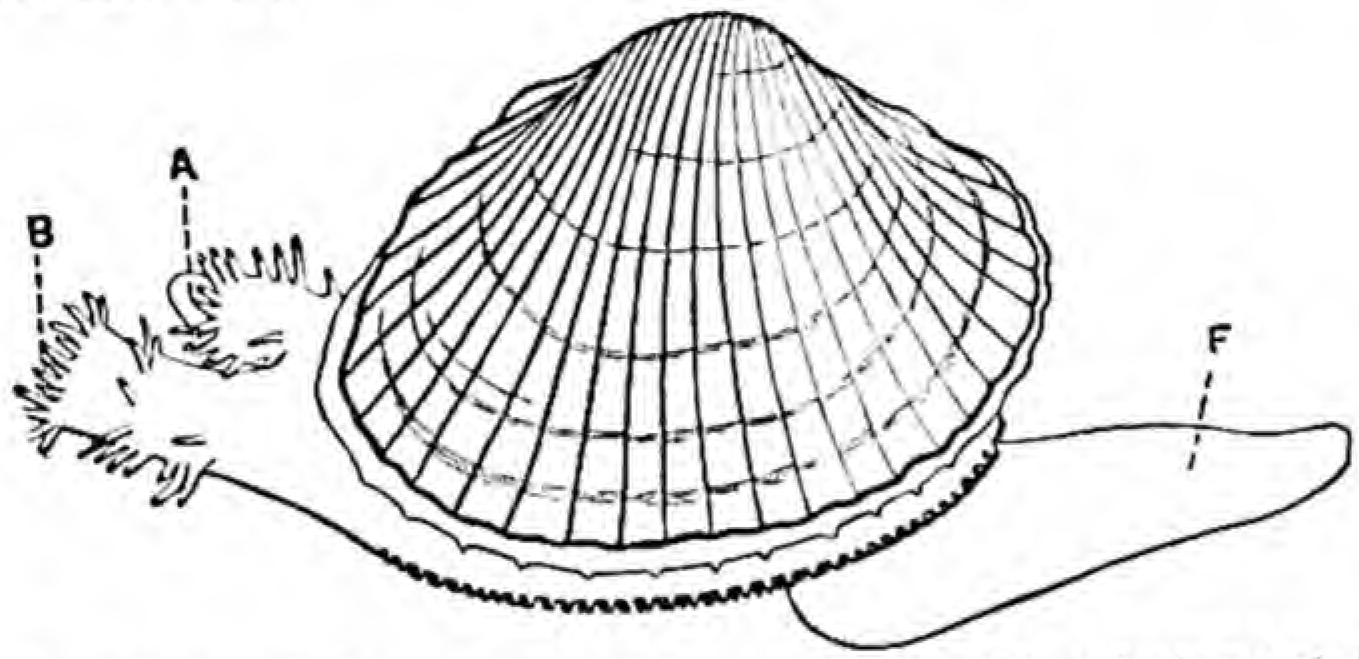


FIG. 594.—**Cardium edule.** *A*, exhalant siphon ; *B*, inhalant siphon ; *F*, foot. (From the *Cambridge Natural History*.)

Anodonta and Unio, as we have seen, the two lobes unite so as to enclose a dorsal or exhalant siphon, a ventral or inhalant siphon being formed simply by apposition of the lobes ventrally. In such cases the pallial muscles in their neighbourhood act as retractors of the short and imperfect tubes thus formed. In other species a second concrescence of the mantle-lobes takes place so as to convert the inhalant siphon into an actual circumscribed aperture or short tube. In the Sinupalliata the two siphons are prolonged into distinct muscular tubes (Fig. 594, *A*, *B*) which, in the position of extension, project beyond the posterior margin of the shell and may even be considerably longer than the body. Under these circumstances the posterior pallial muscles become enlarged to form retractors of the siphons, and the portion of the pallial line from which they arise is, as it were, pushed forwards so as to form a bay or *pallial sinus* (Fig. 595, *p.s.*). Thus the shells of species with well-developed siphons are *sinupalliate*, or have an

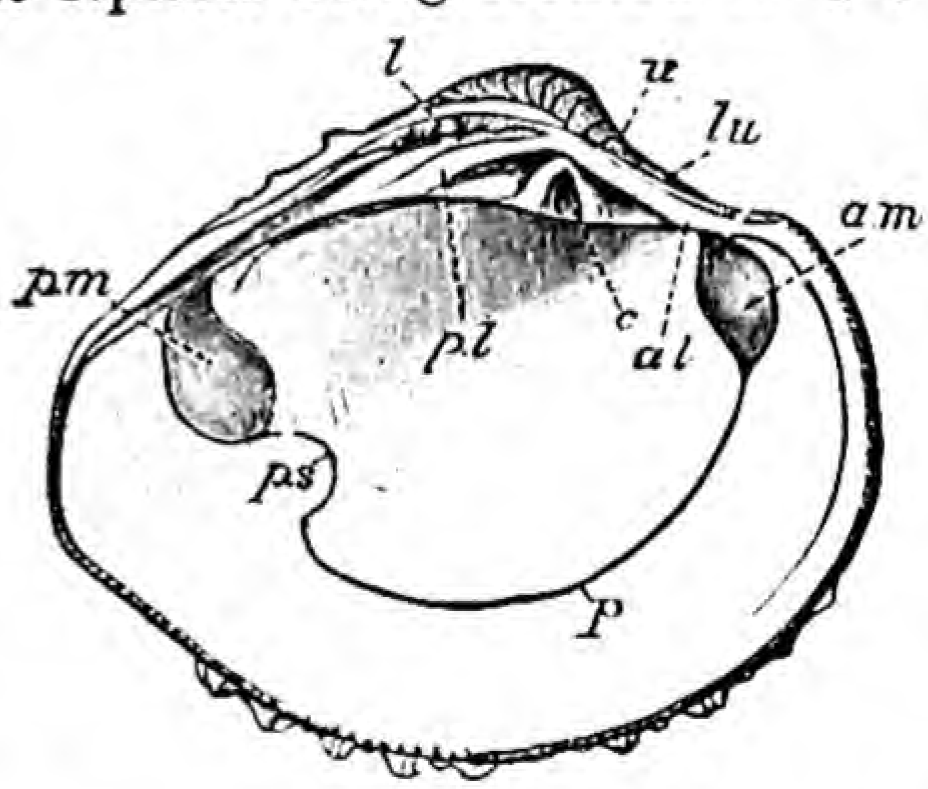


FIG. 595.—**Venus gnidia,** inner surface of left valve. *al*, anterior lateral tooth ; *am*, anterior adductor impression ; *c*. cardinal teeth ; *l*. ligament ; *lu*. lunule ; *p*. pallial line ; *p. l.* posterior lateral tooth ; *p. m.* posterior adductor impression ; *p. s.* pallial sinus ; *u*. umbo. (From the *Cambridge Natural History*.)

indented pallial line, while those with small or no siphons are *integripalliate*, or have an entire pallial line. The larger the siphons the stronger are their muscles and the deeper is the pallial sinus: when very large they

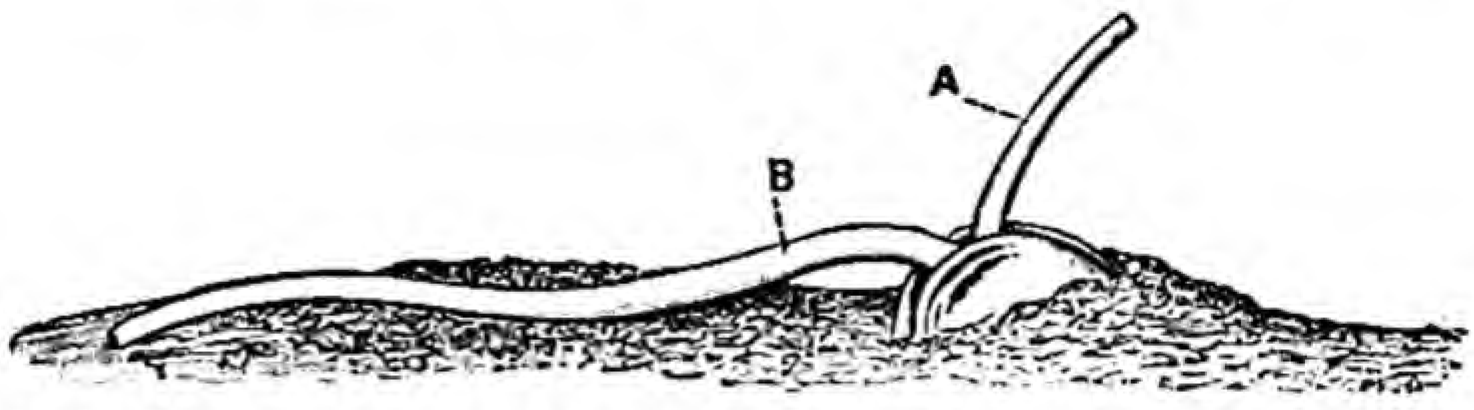


FIG. 596.—**Scrobicularia piperata,** in its natural position, partly buried in sand. *A*, exhalant siphon; *B*, inhalant siphon. (From the *Cambridge Natural History*.)

cannot be completely retracted, and the posterior border of the shell then gapes permanently. The siphons may be separate (Fig. 596) or united (Fig. 597). They are specially adapted for species of burrowing habits, which are able to remain buried in the mud or sand, only the ends of the siphons being exposed for the supply of aërated water and food, and even these can be instantly withdrawn in the event of danger.

FIG. 597.—**Solenocurtus strigilatus.** *s. af*, inhalant siphon, *s. ef*, exhalant siphon, the two united at *SS*. (From the *Cambridge Natural History*.)

In addition to their union posteriorly to form the siphons, the mantle-lobes may concresce to a greater or less extent along their ventral border (Fig. 598), forming a more or less tubular investment for the body, and leaving an anterior *pedal aperture* for the protrusion of the foot. Their anterior portions may also be united to form a sort of hood.

To return to the **shell**, the muscular impressions and the pallial line on which have already been referred to. As a general rule the right and left valves are alike, or nearly so, the shell being therefore *equivalve*. Each valve is *inequilateral*, being divided into unequal portions by a line drawn from the umbo to the gape. It will be seen that in the Brachiopoda (*vide* Section X), the precise opposite is the case, the shell being equilateral and inequivalved. Some Pseudolamellibranchiata are, however, nearly equilateral and markedly inequivalved, such as the Scallop (*Pecten*), and the inequivalve character is still more marked in the Oyster, in which the right valve is deeply concavo-convex and permanently attached to a rock, while the left is flat and forms a sort of lid. This condition of things reaches its maximum in the extinct *Hippurites* (Fig. 599, *B*), in which the left valve has the form of a long tube closed at one end by the flat lid-like right valve. In the extinct *Requienia* (*A*) the left valve is spirally coiled, so that

it resembles a snail-shell, and its aperture is closed by the flat lid-like right valve: in *Diceras*, also extinct, both valves are coiled.

The hinge-teeth (Fig. 595) vary greatly in form and size or may be absent altogether: the hinge-ligament is usually band-like, but in Pecten takes the

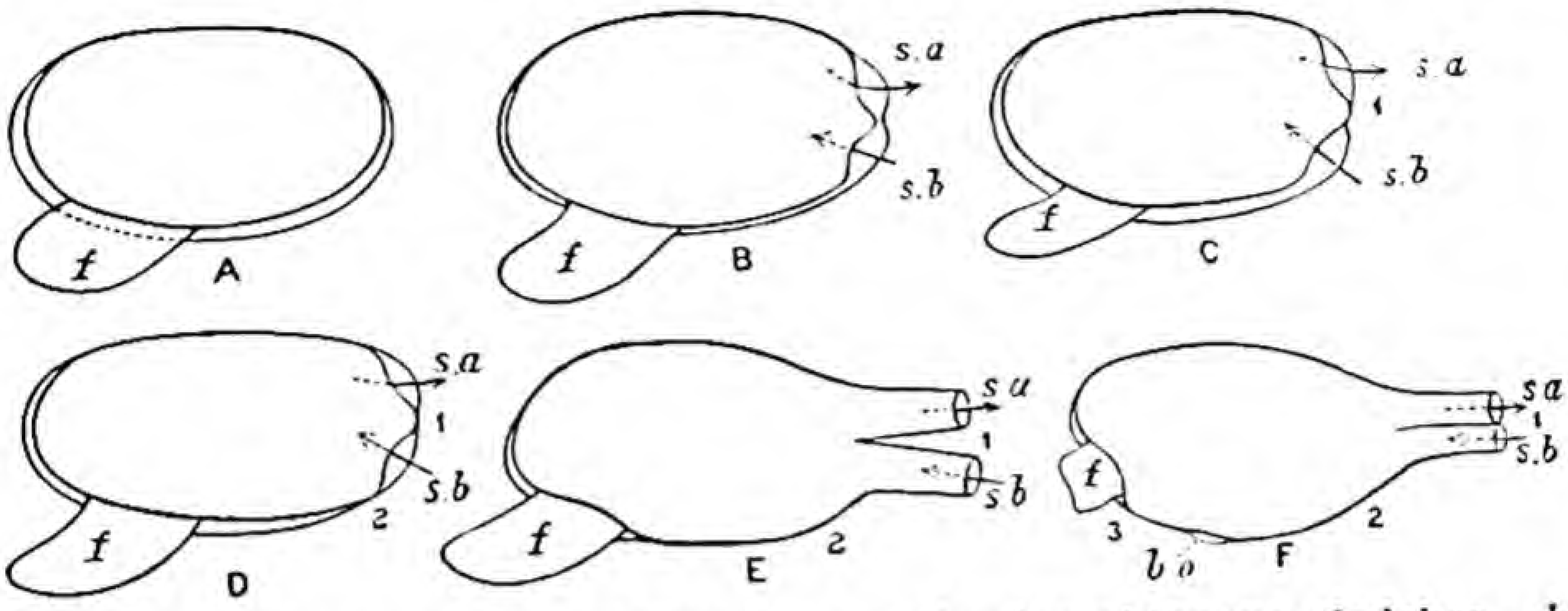


FIG. 598.—Diagram illustrating the various degrees of union of the mantle-lobes. *b. o.* byssal aperture; *f.* foot; *s. a*, exhalant siphon; *s. b*, inhalant siphon; *1*, first point of union between siphons; *2*, second, between inhalant siphon and foot; *3*, third, between byssal aperture and foot. (From the *Cambridge Natural History*.)

form of a cylindrical cord. The variations in form, ornamentation, colour, etc., among the many thousand known species of shell are too numerous to mention; but reference must be made to peculiar modifications found in certain burrowing forms. In *Pholas*, a siphonate genus which burrows in stone, the shell is weak and brittle, and additional calcareous pieces are developed between the two valves. In *Teredo* (Fig. 600), the so-called Ship-worm, which causes great destruction by boring into piles, ships' timbers, etc., the valves (*V.*) remain very small and weak but movable, and the general surface of the mantle secretes a continuous shelly tube which lines the burrow. In *Brechites* (*Aspergillum*) (Fig. 601), which lives buried in sand, there is a similar but wider calcareous tube, with which the valves are completely fused, and the anterior end of the tube which appears above the surface of the sand is closed by a plate perforated with numerous holes like the rose of a watering-pot. The larval shell is sometimes, though not always, distinguishable at the apex of each valve in the Bivalvia in general.

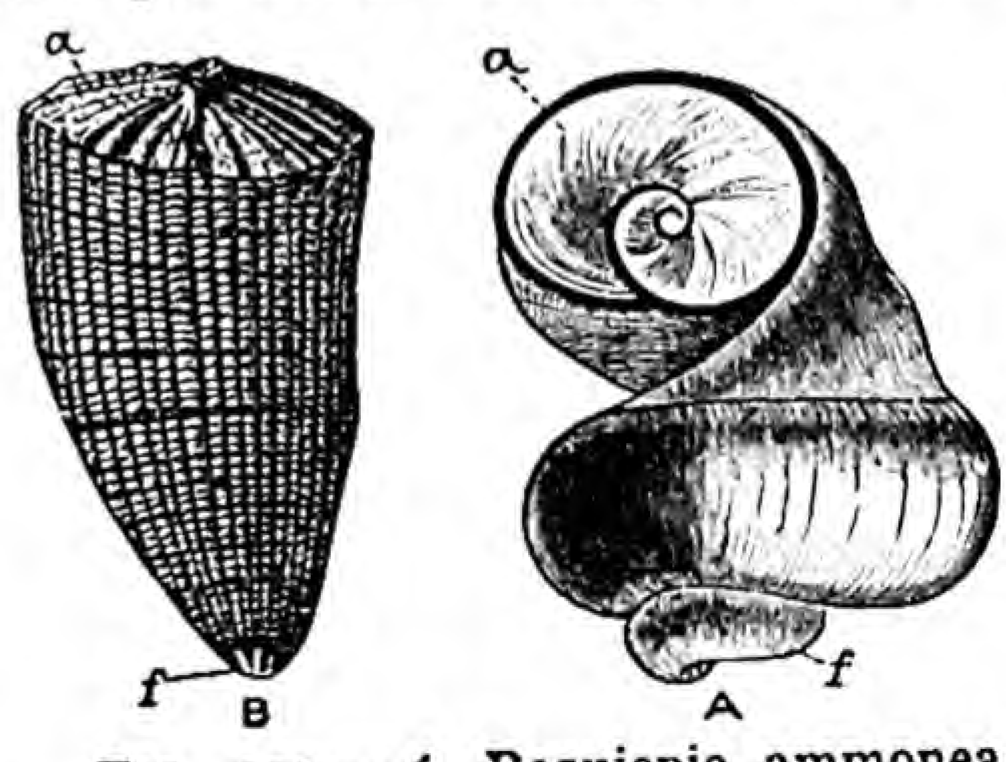


FIG. 599.—*A*, **Requienia ammonea**; *B*, **Hippurites cornu-vaccinum.** *a*, right valve; *f*, point of fixation. (From the *Cambridge Natural History*.)

In *Nucula*, *Arca*, etc., the **foot** (Fig. 603, *f.*) presents what may be considered as its most primitive form, having a flat ventral surface of sole upon which the animal creeps. Far more common is the ploughshare-like form we are already

familiar with in Anodonta and Unio, adapted for slowly making its way through sand or mud. In a few forms, *e.g.*, Trigonia and Cardium (Fig. 594), it is bent upon itself and is capable of being suddenly straightened so as to act as a leaping organ: in Mytilus it is cylindrical (Fig. 602, *F*): in the Oyster it is absent. In addition to the anterior and posterior retractors and a pair of *protractors*, the foot is sometimes provided with a *levator* muscle, particularly well developed in Nucula and its allies.

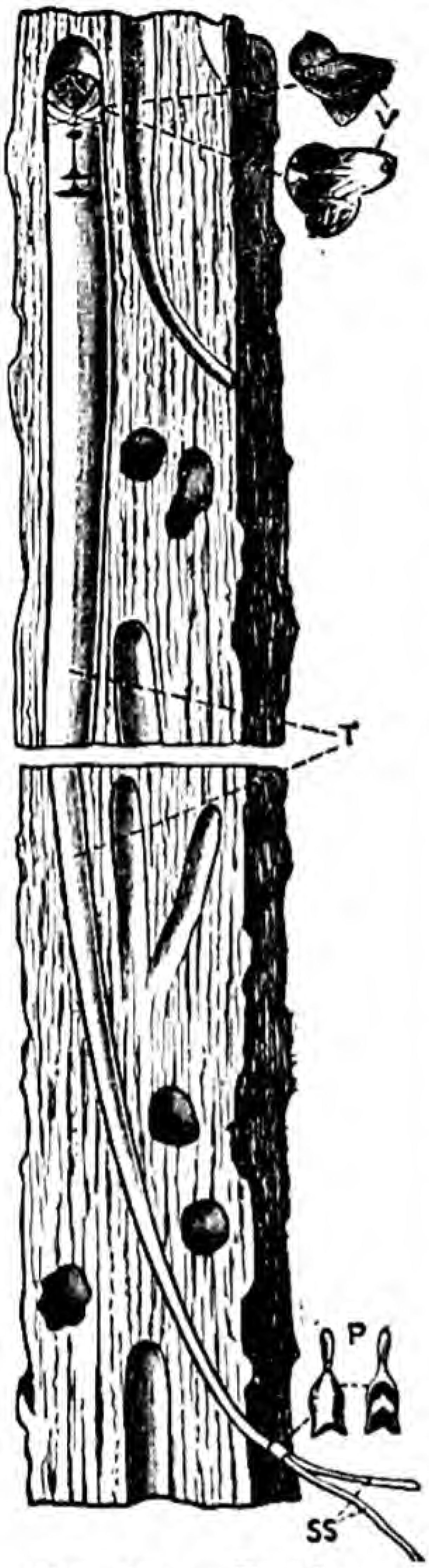


FIG. 600.—**Teredo navalis**, in a piece of timber. *P*, pallets (small calcareous plates supporting the siphons); *SS*. siphons; *T*, tube; *V*, valve of shell. (From the *Cambridge Natural History*.)

Immediately posterior to the foot a **byssus-gland** is frequently found: it secretes a silky substance in the form of threads which serve to anchor the animal permanently or temporarily. It is by means of the byssus that the Sea-mussel (*Mytilus*) is attached to the rocks (Fig. 602, *By*): in *Pinna* the threads are fine enough to be woven in a fabric. In *Lima* the threads of the byssus are spun into a kind of nest in which the animals lie protected, and in species of *Modiola* similar modifications of the byssus occur. In such forms as Mytilus the muscles which ordinarily serve to retract the foot are inserted mainly into the byssus: the latter being fixed, they serve to rotate the animal in various directions, or, in other words, act as *adjustors* and also as *retractors* of the byssus. It must be borne in mind that the definite byssus just described is not homologous with the provisional byssus of Anodonta (p. 591) which lies in front of the mouth.

The **gills** or **ctenidia** are two in number, right and left. Each consists of a horizontal axis bearing two rows of filaments, outer and inner, which are outgrowths from it. In the Protobranchiata (*e.g.*, Nucula) the filaments are short, compressed, and free from one another (Figs. 603, *g*, and 604, *A*). In *Amusium* (*B*) the gill-filaments are much elongated and thread-like instead of triangular.

In the common Ark-shell (*Arca*, *C*) a great change is seen. The gill-filaments are delicate and somewhat flattened threads, each bent upon itself into the form of an elongated U, and therefore consisting of a proximal or fixed limb and a distal or free limb. The flexure takes place in such a way that the free limb is external in the outer row of filaments, internal in the inner row. Adjacent filaments are loosely united by groups of large interlocking cilia (see Fig. 605),

FIG. 601.—**Aspergillum.** (After Sowerby.)

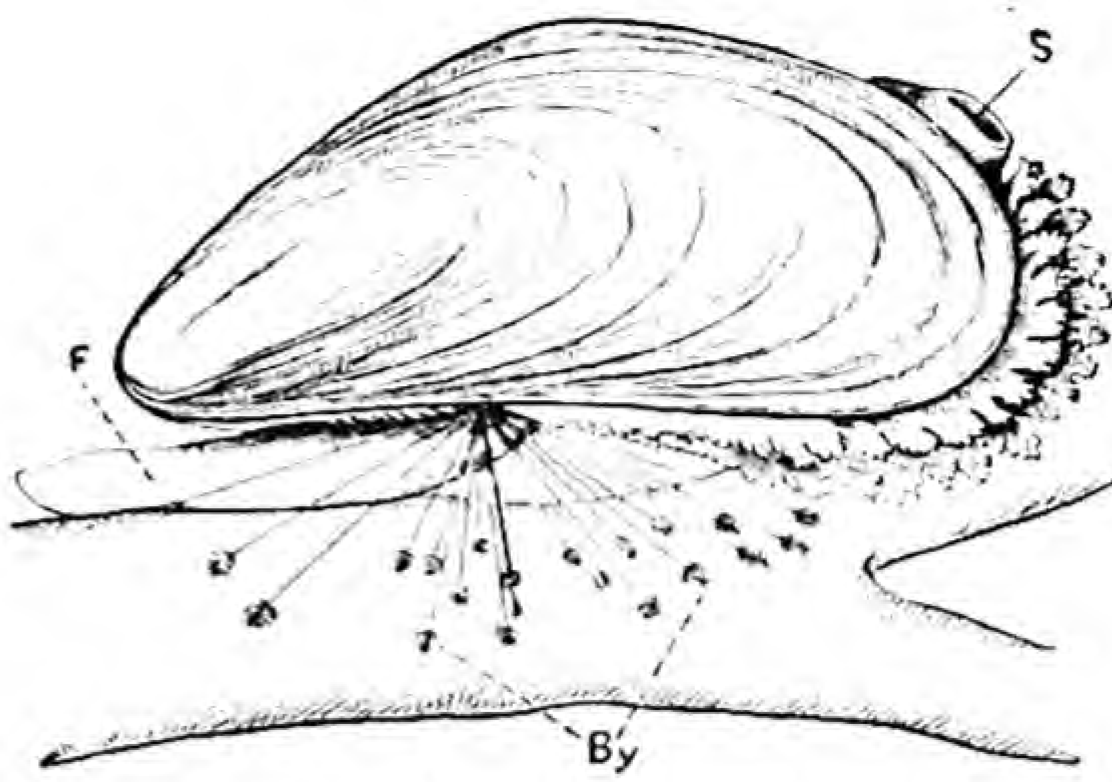


FIG. 602.—**Mytilus edulis,** attached by byssus (By.) to a piece of wood. *F*, foot; *S*, exhalant siphon. (From the *Cambridge Natural History*.)

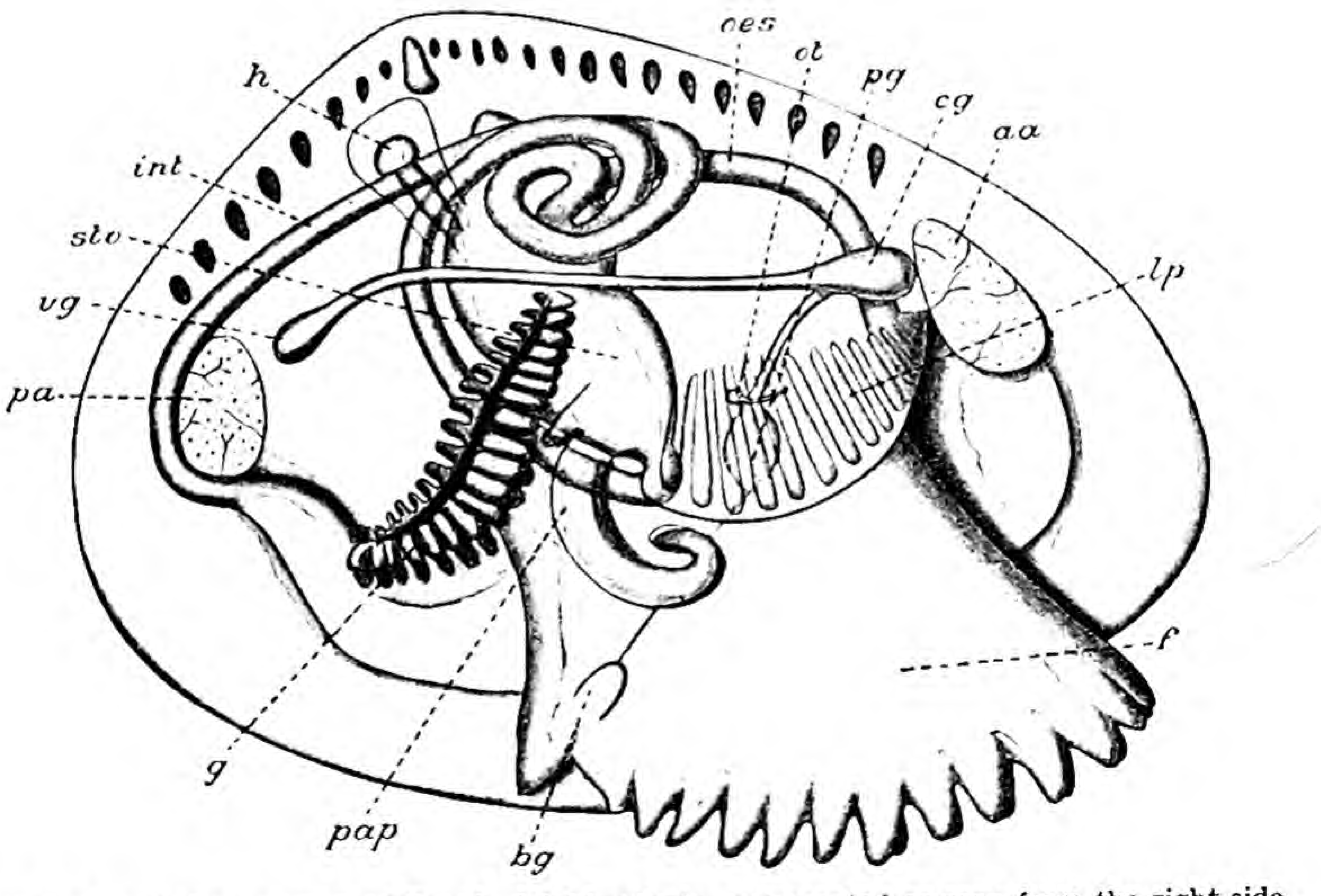


FIG. 603.—Adult specimen of **Nucula delphinodonta,** represented as seen from the right side. Reconstructed to show internal organs. Fully grown specimens are 4 mm. long. *aa.* anterior adductor muscle; *bg.* byssal gland; *cg.* cerebral ganglion; *f.* foot; *g.* gill; *h.* heart; *int.* intestine; *lp.* labial palp; *œs.* œsophagus; *ot.* statocyst; *pa.* posterior adductor muscle; *pap.* palp appendage; *pg.* pedal ganglion; *sto.* stomach; *vg.* visceral ganglion. (After Drew.)

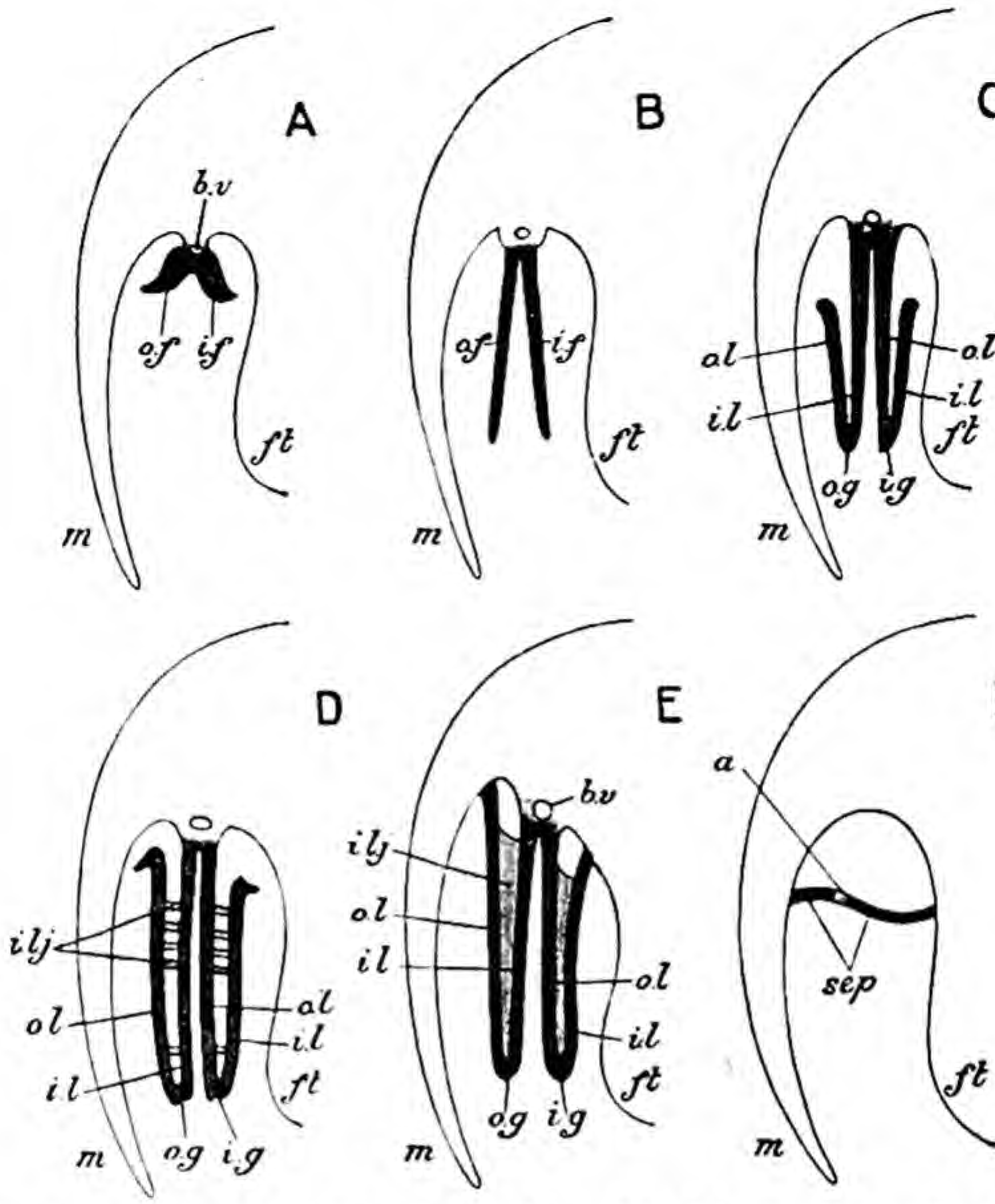


Fig. 604.—Half transverse sections of various *Bivalvia* to show the chief kinds of gill. *A*, **Nucula**; *B*, **Amusium**; *C*, **Arca**; *D*, **Mytilus**; *E*, **Anodonta**; *F*, **Poromya**. *a.* aperture in branchial septum; *b. v.* blood-vessel; *ft.* foot; *i. f.* inner row of filaments; *i. g.* inner lamina; *i. l.* inner lamella; *i. l. j.* interlamellar junctions; *m.* mantle; *o. f.* outer row of filaments; *o. g.* outer lamina; *o. l.* outer lamella; *sep.* branchial septum. (Modified from Korschelt and Heider, and Lang.)

placed at regular intervals, and in this way all the outer and all the inner limbs of the filaments are respectively joined together so as to convert each longitudinal row of U-shaped filaments into a double plate, fairly coherent unless the ciliary junctions are forcibly separated. In this way the single ctenidium of Nucula has given place to two plate-like simple laminæ, each formed of an outer and an inner lamella: the inner lamella of the outer and the outer lamella of the inner laminæ are united along their dorsal edges, the line of junction representing the axis of the ctenidium: the outer lamella of the outer and the inner lamella of the inner laminæ are free dorsally.

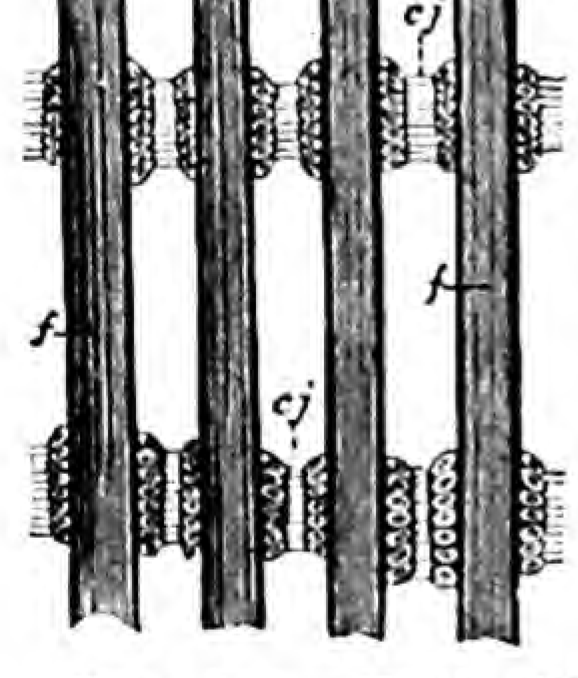


Fig. 605.—Four gill-filaments of **Mytilus**. *c. j.* ciliary junction; *f.* filaments. (From the *Cambridge Natural History*.)

In *Mytilus* (Fig. 604, *D*) the gill is strengthened by the development of delicate non-vascular bars or interlamellar junctions between the two limbs of each

filament. In *Lucina* these junctions are large and provided with blood-vessels; and vascular bars of tissue, the interfilamentar junctions, replace the ciliary junctions of the lower forms. Thus by a regular series of gradations the ctenidium is replaced by the complex double gill we are already familiar with in Anodonta. In all the higher forms the outer lamella of the outer lamina unites with the mantle and the inner lamella of the inner lamina with the visceral mass, while, posterior to the latter, the inner lamellæ of the right and left inner laminæ unite with one another. The blood-vessels, which are confined to the filaments in the simpler types, occur also in the interfilamentar and interlamellar junctions in the more complex forms of gills. In the Septibranchiata the gills are degenerate, being represented by a horizontal muscular partition or septum (Fig. 604, *F*, and Fig. 606, IX), which divides the inhalant

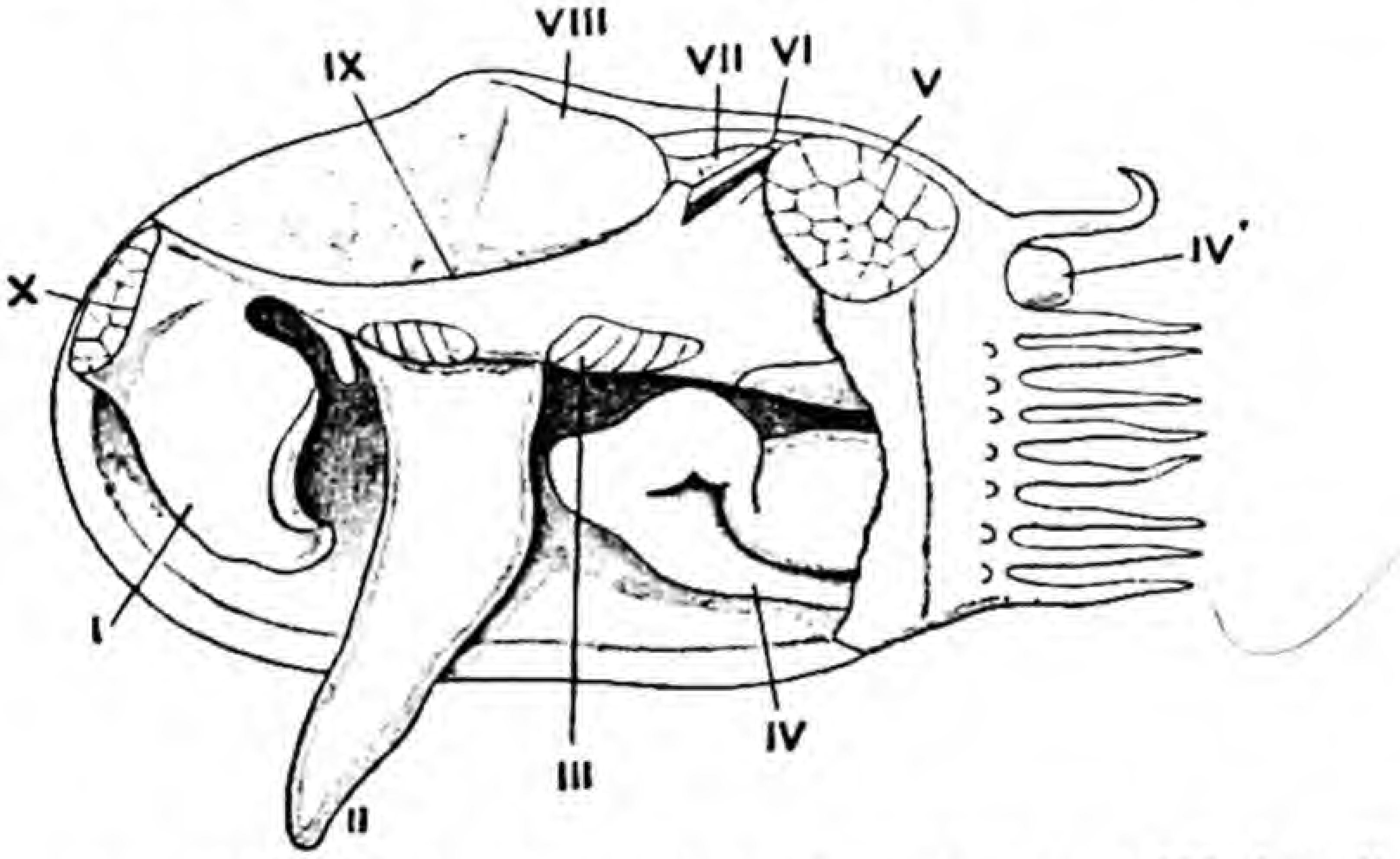


FIG. 606.—Dissection of **Poromya.** I, anterior palp; II, foot; III, lamella on branchial septum; IV, valve of branchial aperture; IV′, anal siphon; V, posterior adductor; VI, posterior retractor of foot; VII, heart; VIII, ovary; IX, branchial septum; X, anterior adductor. (From Pelseneer.)

and exhalant chambers from one another. Respiration in this case is performed entirely by the internal face of the mantle.

Digestive organs.—The mouth is anterior; in forms with two adductor muscles it is always placed immediately behind the anterior adductor. It is usually bounded by two pairs of labial palps which sometimes attain a relatively immense size (Fig. 603); there is never any trace of jaws or other masticatory apparatus. The convolutions of the intestine are sometimes very complex. The crystalline style either lies freely in the stomach and anterior part of the intestine, or is contained in a cæcal pouch of the stomach (Fig. 607), which may be prolonged into one of the lobes of the mantle.

By the action of cilia the crystalline style is rotated and at the same time moved forward, while its free end which projects into the stomach is constantly worn away by friction with the gastric shield, a cuticular thickening of the wall

of the stomach (Fig. 607, *V.*). The substance of the style contains an *amylase* for the digestion of carbo-hydrates.

The **excretory organs** or **kidneys** occur in their simplest form in the Protobranchiata, in which they have the form of cylindrical curved tubes, opening at one end into the pericardium and at the other on to the exterior; the whole organ is lined with glandular epithelium, and has no communication with its fellow of the opposite side. In the higher forms the organ becomes differentiated into a secreting portion or kidney, which is very spongy in texture, and opens into the pericardium, and a non-secretory portion or bladder, which opens externally. Frequently there is a communication between the right and left kidneys, and in some genera, such as the Oyster, the organs become exten-

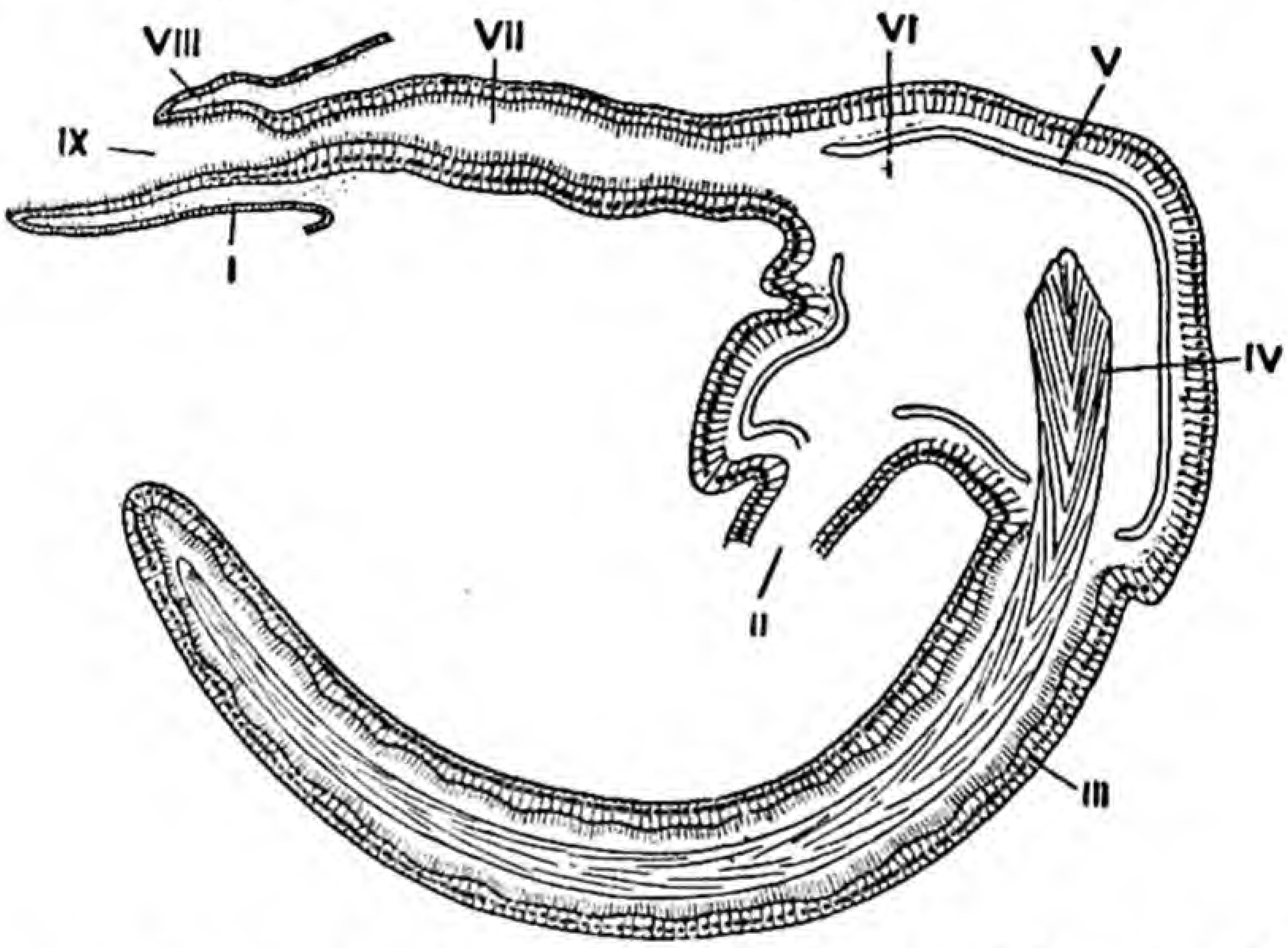


FIG. 607.—Sagittal section of part of enteric canal of **Donax.** I, lower lip; II, intestine; III, pyloric cæcum; IV, crystalline style; V, cuticle; VI, stomach; VII, gullet; VIII, upper lip; IX, mouth. (From Pelseneer.)

sively branched. Also taking a share in the process of excretion are the *pericardial glands*, or *Keber's organs*, glandular developments of the wall of the pericardium.

Circulatory Organs.—The heart is usually perforated by the rectum, but lies altogether above it in Nucula (Fig. 603, *h.*) and some other genera; the ordinary arrangement seems to have been brought about by the heart becoming folded over the intestine and united below it. In the Oyster and some other forms the heart is below the rectum. In Arca the ventricle is divided into two by a constriction. Pores are often found on the surface of the foot, and it has been asserted that through them the external water mixes with the blood; this, however, is certainly not the case: the blood-system is everywhere closed. The blood is red in some forms (*e.g.*, *Arca*) owing to the presence of hæmoglobin; in some cases it is of a bluish tint owing to the presence of hæmocyanin.

The nervous system is found in its most primitive condition in Nucula (Fig. 608). Instead of the single cerebro-pleural ganglion of Anodonta there are, on each side, distinct cerebral (XVI) and pleural (I) ganglia, each united by a connective with the pedal.

The most characteristic **sense-organs** are the statocysts and the osphradia. The *statocyst* is always placed in the foot, in close relation to the pedal ganglion, sometimes embedded in the latter. The statocysts are developed as involutions of the ectoderm and retain their connection with the exterior in Nucula (Fig. 603, *ot.*) and some others. In most cases they become closed sacs. The cavity is usually ciliated, but the cilia may be wanting. Each statocyst may contain a number of minute *statocones* or, more usually, a single, larger *statolith*. The nerves supplying the statocysts are given off not from the pedal ganglia, but from the cerebro-pedal connectives, and their fibres are derived from the cerebro-pleural ganglia.

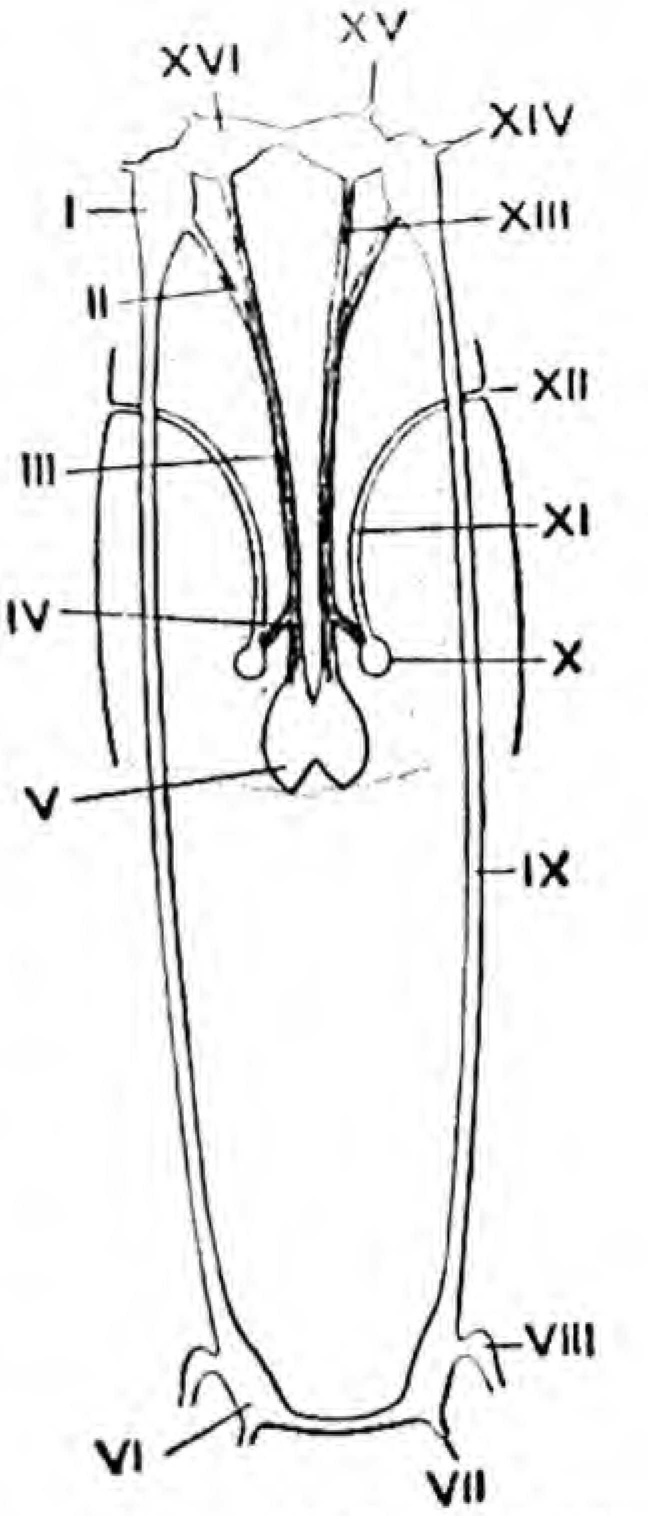


FIG. 608.—Nervous system and static organs of **Nucula**. I, pleural ganglion; II, pleuropedal connective; III, common connective from cerebral and pleural to pedal ganglia; IV, static nerve; V, pedal ganglion; VI, visceral ganglion; VII, posterior pallial nerve; VIII, osphradial ganglion; IX, visceral connective; X, statocyst; XI, canal of statocyst; XII, its external aperture; XIII, cerebro-pedal connective; XIV, anterior pallial nerve; XV, nerve to palps; XVI, cerebral ganglion. (From Pelseneer.)

The *osphradia*—" olfactory " or water-testing organs—are patches of sensory epithelium with an accessory or osphradial ganglion situated in immediate relation with the visceral ganglia (Fig. 608, VIII), but connected by nerve-fibres with the cerebro-pleural ganglia. Patches of sensory epithelium, very similar to the osphradia, and called the *abdominal sense-organs*, occur one on each side of the anus in Arca and other forms devoid of siphons, and a similar organ has been described beside the retractor muscles of the siphons in several Sinupalliata.

In a few instances *eyes* are present, but never in what we are accustomed to consider as the normal position for such organs, at the anterior or head-end of the body. They occur, in fact, in the only situation where they can be of any use, namely, along the edge of the mantle. The best-known form in which they occur is the common Scallop (*Pecten*), which has a single row (Fig. 592, VII) all round the mantle-border. Each has a cornea (Fig. 609, *co.*), a cellular (not cuticular) lens (*l.*), a retina (*re.*$_1$, *re.*$_2$)—formed of cells, the inner ends of which are modified into visual rods (*v. r.*), and an optic nerve (*n.*$_1$, *n.*$_2$), one branch of which spreads over the front of the retina and sends branches backwards to the visual rods. In this peculiarity, as well as in the cellular lens, the eye of Pecten is singularly like

that of Vertebrates. The pallial eyes of Bivalvia are probably to be looked upon as modified tentacles.

Reproduction and Development.—Most Bivalvia are diœcious, but several hermaphrodite forms are known. Some of these, such as some Oysters, are protandrous, the gonad producing first sperms and afterwards ova: in others part of the gonad serves as an ovary, part as a testis, the two opening into a common duct: in others again there is a distinct ovary and testis on each side opening by separate ducts. There are never any accessory organs of reproduction, such as spermatheca, penis, etc. Fertilization frequently takes

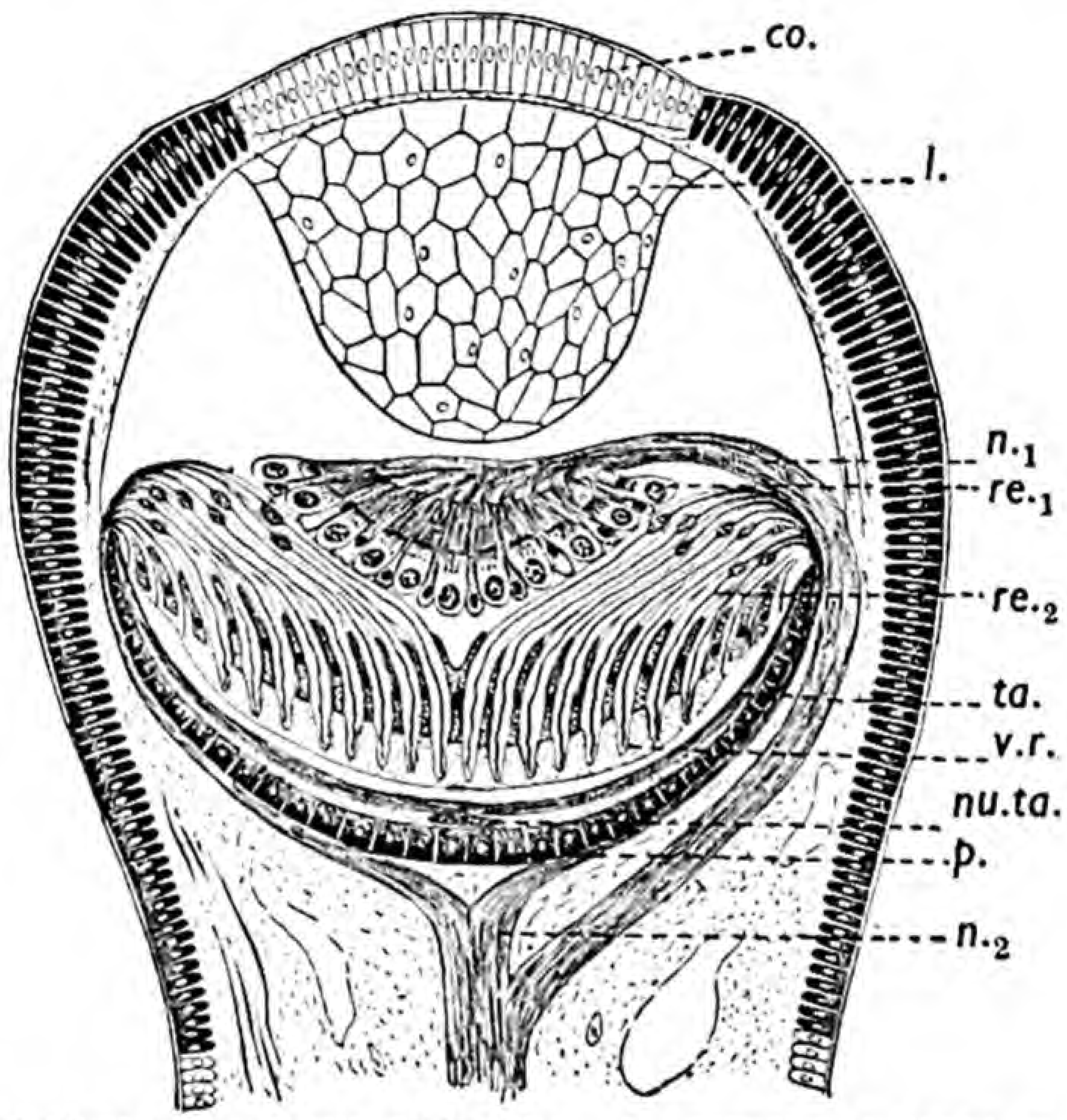


FIG. 609.—Vertical section of eye of **Pecten.** *co.* cornea; *l.* lens; $n._1$ and $n._2$ distal and proximal nerve-branches; *nu. ta.* nucleus of tapetum-cell; *p.* pigment layer; $re._1$ and $re._2$ distal and proximal retinæ; *ta.* tapetum; *v. r.* visual rod. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Küpfer.)

place in the water after the eggs are laid. Cleavage is total and follows the spiral type. One of the four macromeres is very much larger than the other three. The gastrula is formed either by invagination or by epiboly. A shell-gland (Fig. 610, *sd.*) is formed as an invagination of the dorsal surface, a stomodæum (*m.*) as an invagination of the ventral surface, and the larva of most forms, unlike that of Anodonta or Unio, passes into a stage in which it closely resembles the trochophore of Chætopods, having a prototroch and an apical tuft in the middle of the prostomium (Fig. 610). There is also an ecto-dermal thickening on the prostomium which becomes the cerebral ganglion, and a similar ventral thickening which gives rise to the pedal ganglion and corresponds with the rudiment of the ventral nerve-cord in Polychæta. The

trochophore of the Bivalvia is, however, distinguished from the corresponding stage in Worms by the presence of the shell-gland, which soon secretes an

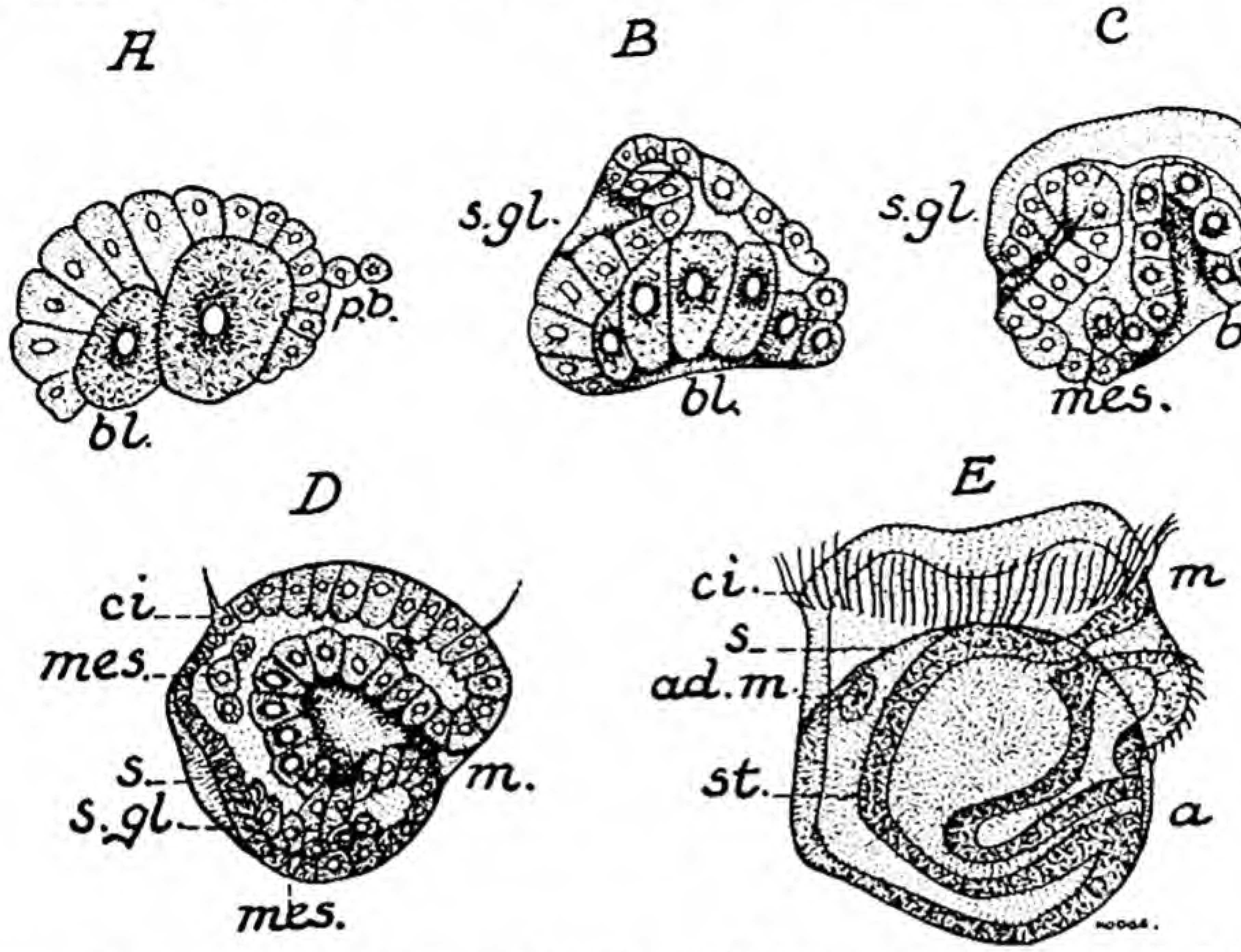


FIG. 610.—Five stages in the development of **Ostrea.** *a.* anus; *ad. m.* anterior adductor muscle; *bl.* blastopore; *ci.* pre-oral circlet of cilia; *m.* mouth; *mes.* mesoderm; *p. b.* polar bodies; *s.* shell; *s. gl.* shell gland; *st.* stomach. (After Korschelt and Heider.)

unpaired shell. The prostomial region grows out into a thickened retractile rim bearing the pre-oral circlet of cilia, and called the *velum* (Fig. 611, *vel.*): the larva at this stage is distinguished as a *veliger*—a very characteristic mulluscan phase of development. The shell soon becomes bivalved and extends ventrally on each side, paired processes of the dorsal region of the body accompanying it and forming the mantle-lobes. A projection grows out from the ventral surface, between mouth and anus, and forms the foot (Fig. 612, *f.*), and on the sides of the body the gill-filaments (*gi.*) arise as a row of fine processes, at first simple but afterwards becoming bent upon themselves so as to assume a V-shape. Eyes are often present in the larva at the base of the velum.

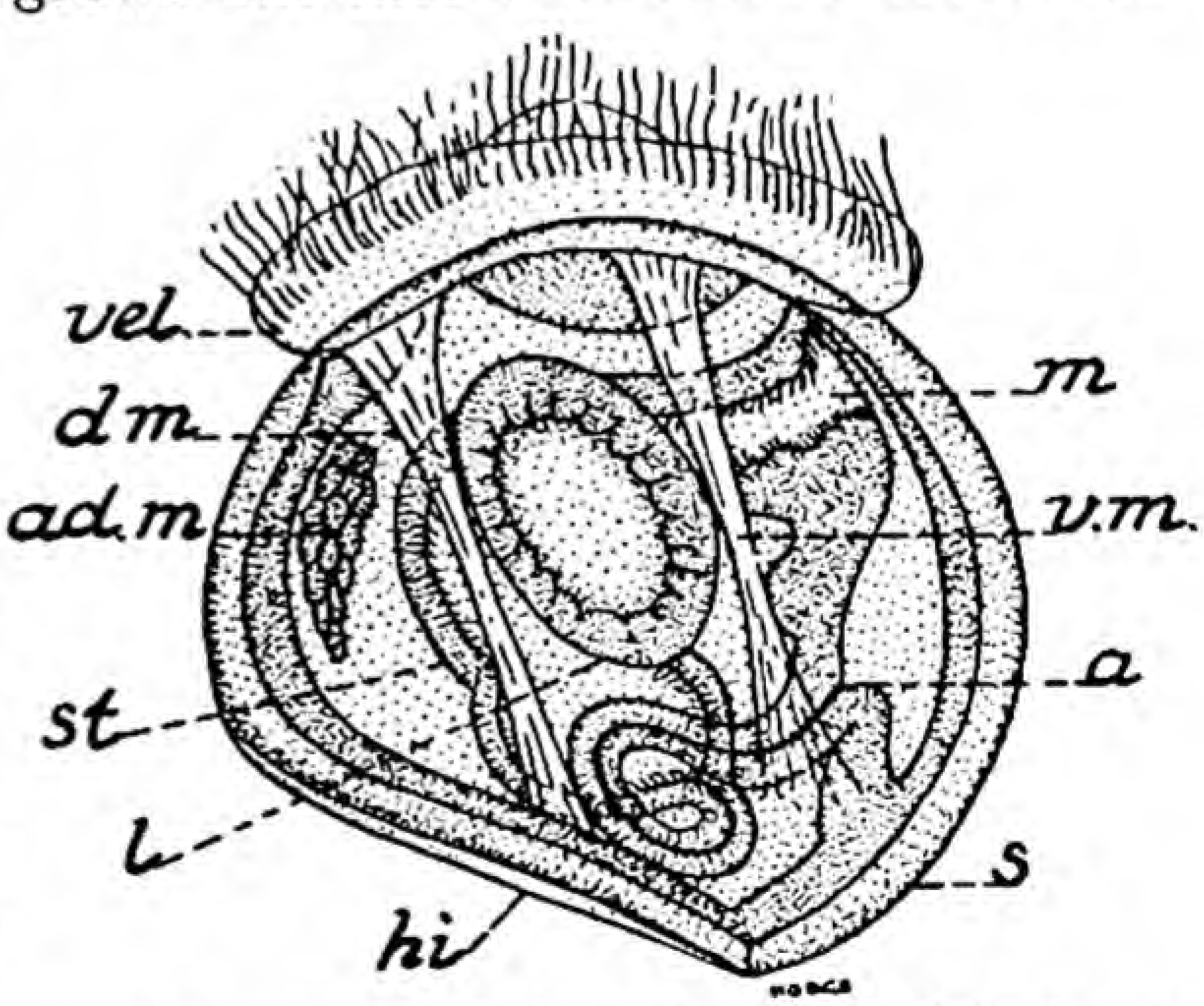


FIG. 611.—Veliger larva of **Ostrea.** *a.* anus; *ad. m.* adductor muscle; *d. m.* dorsal longitudinal muscle; *hi.* hinge of shell; *l.* "liver"; *m.* mouth; *s.* shell; *st.* stomach; *vel.* velum; *v. m.* ventral longitudinal muscle. (After Korschelt and Heider.)

General Remarks.—Although none of the Bivalvia are microscopic, they

present a considerable range in size, from the minute *Nucula*, about 4 mm. long, to the Giant Clam (*Tridacna gigas*) of the Indian and Pacific islands, which is sometimes 60 cm. (two feet) in length and 500 pounds in weight.

Many shells are white or dull brown in colour, but in several genera brilliant tints are the rule, the various species of Scallop (*Pecten*) being specially remarkable in this respect. The inner surface of the shell often exhibits beautiful iridescent tints, noticeably in the so-called Pearl-oyster (*Meleagrina*) and the Australian *Trigonia*. In this connection the formation of *pearls* by some species must be mentioned: they are deposits of nacre formed usually round encysted parasitic worms, either between the mantle and shell or in the soft parts. They are produced, amongst other species, by the "Pearl-oyster"

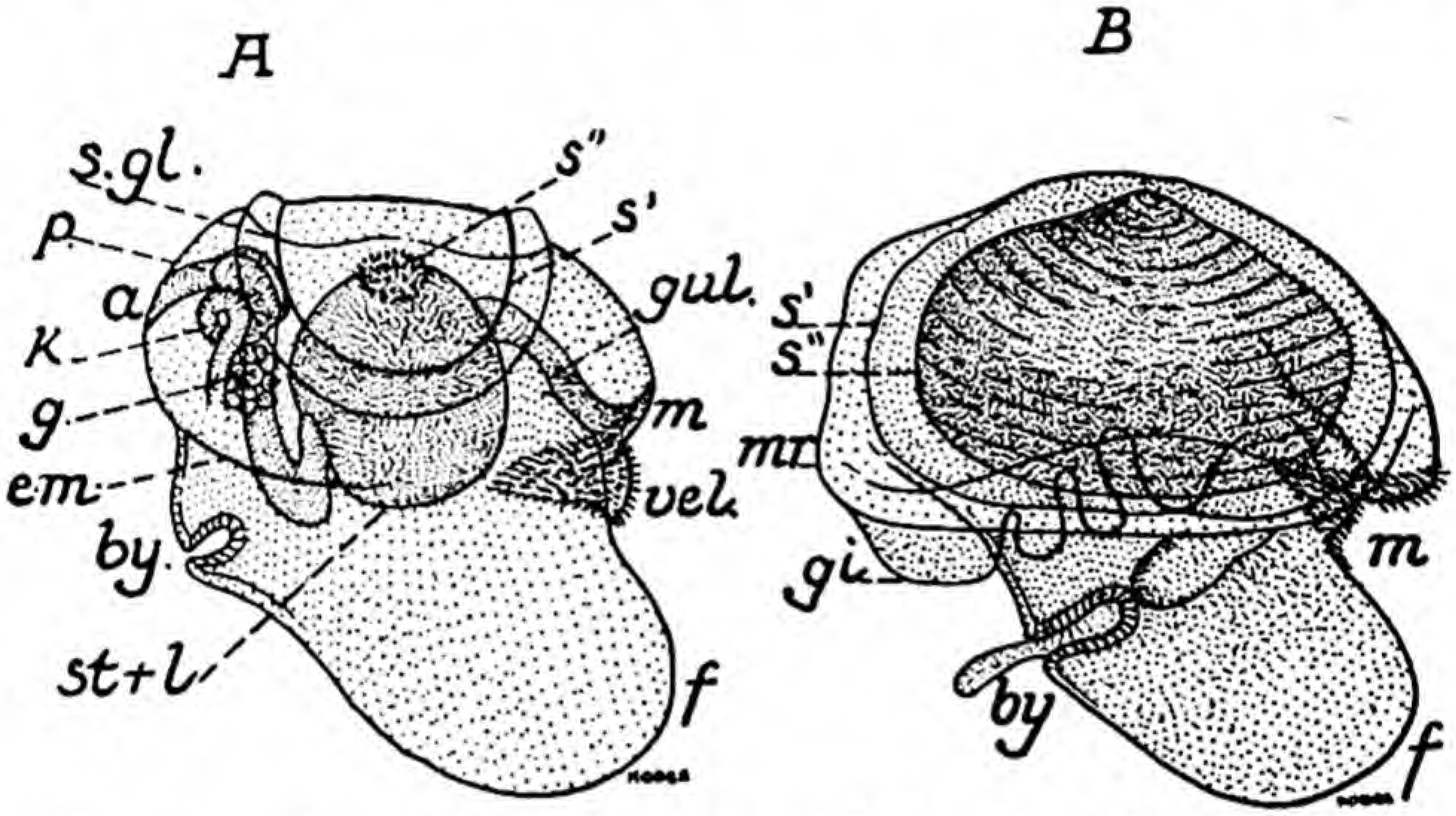


FIG. 612.—Two embryos of **Sphærium.** *a.* anus; *by.* byssus-gland; *e. m., mr.* edge of mantle; *f.* foot; *g.* gonad; *gi.* gill; *gul.* gullet; *k.* kidney; *p.* pericardium; *s'.* unpaired shell; *s''.* rudiment of paired shell; *s. gl.* shell gland; *st.* + *l.* stomach and "liver"; *vel.* velar æerea. (After Korschelt and Heider.)

(*Meleagrina margaritifera*) and by the Pearl-mussel (*Unio margaritifera*). Some species, such as the common boring *Pholas*, are luminescent.

Most Bivalvia are sluggish in habit, progressing only by slow contractions of the foot, and some are permanently fixed during adult life by the byssus, or are only able to change their position after throwing off the byssus, which becomes replaced by a new one. The Scallops, however, swim freely by clapping the valves together. The Cockles (*Cardium*), *Trigonia*, etc., jump by sudden movements of the foot, and the Razor-fish (*Solen*) jerks itself forward by suddenly withdrawing its foot and thus ejecting water through the siphons. The only parasitic genus is *Entovalva*, found in the gullet of a Holothurian.

Bivalvia are abundant both in fresh water and the sea; the marine forms are mainly littoral. None are pelagic or terrestrial. They are very abundant in the fossil condition, occurring in all formations from the Lower Cambrian upwards, and, owing to their gregarious habits, frequently forming extensive

deposits or shell-beds. The oldest forms are all iso- or hetero-myarian; the monomyarian types (Pseudolamellibranchiata) appear first in the Carboniferous and the Siphoniata not until the Triassic period. The modern genus *Arca* dates from the Upper Cambrian, and thus furnishes as striking an example of a "persistent type" as some of the Brachiopods.

There seems to be little doubt that the Protobranchiata, and especially Nucula, exhibit the most primitive type of organization, as indicated by the plume-like gills with separate filaments, the simple kidneys, and the distinct cerebral and pleural ganglia; absence of concrescence is always a mark of low or generalized organization. The Filibranchiata with imperfectly united gill-filaments come next, and are divisible into two groups—isomyarian with equal-sized adductors, and heteromyarian with more or less atrophied anterior and proportionally enlarged posterior adductor; the latter group is to be looked upon as the more specialized, and leads to the Pseudolamellibranchiata (monomyarian type) in which the anterior adductor disappears completely in the adult, while the posterior is immensely enlarged and assumes a central position. Similarly, the isomyarian Filibranchiata lead to the Eulamellibranchiata, which are equal-muscled, but have the gill-filaments united into a complete basket-work. In the Eulamellibranchiata, lastly, there is a gradual series of stages from comparatively generalized forms with free mantle-lobes up to the highly specialized species with large siphons. That the Pseudolamellibranchiata and the siphoniate Eulamellibranchiata are to be looked upon as the highest members of the class is indicated not only by morphological evidence, but by their comparatively late appearance in time.

Class VI.—CEPHALOPODA (SIPHONOPODA).

The *Cephalopoda*, including the Cuttle-fishes, Squids, Octopods, and Nautili, are marine Mollusca of a high grade of organization. There is a very definitely-formed head, bearing a pair of highly-developed eyes, and surrounded by the anterior portion of the foot, modified into arms or tentacles. The body is bilaterally symmetrical. The posterior part of the foot is modified to form a funnel or *siphon* leading out from the large mantle-cavity. A shell is sometimes present, sometimes absent. When present it is usually internal, but sometimes external, and in the Nautili is capable of containing the body of the animal.

1. Examples of the Class.

a. The Cuttle-Fish (*Sepia* [1]).

Cuttle-fishes are marine Molluscs, which live usually at a depth of a few fathoms, but often come into shallower water, and are frequently caught in the

[1] Most of the figures have reference to a common Australian species—*S. cultrata*—but the differences between the various species of the genus are slight and unimportant, and the description given will apply fairly well to any other species.

trawl or the seine. The animal arrests attention when compared with Unio or Triton by the strength, and more particularly the rapidity, of its movements; by the possession of a pair of eyes resembling in size and complexity those of a Fish; and by various other features, all pointing to a higher grade of organization than is attained by the members of the classes of Mollusca dealt with in the preceding pages.

External Features.—The Cuttle-fish (Fig. 613) has a distinct *head*, bearing ten long arms, and a pair of large, highly-developed eyes. The head is connected with the body by a constricted region or *neck*. The *trunk* is elongated and shield-shaped, the base of the shield being towards the head. The long axes of head and trunk are in line with one another. Not only the head, but also the trunk, is completely equilateral, in which respect there is a marked contrast to Triton; and this symmetry extends to most of the systems of internal organs. The free extremity of the head bears the mouth, and is accordingly termed the *oral* extremity, the opposite extremity, the apex of the shield-shaped body, is the *aboral* end. The surfaces of the shield are *anterior* or *antero-dorsal* and *posterior* or *postero-ventral*, its borders *right* and *left*. The anterior surface is to be distinguished by its darker colour, and by the firmness of the body-wall, due to the presence in this position of a hard internal shell.

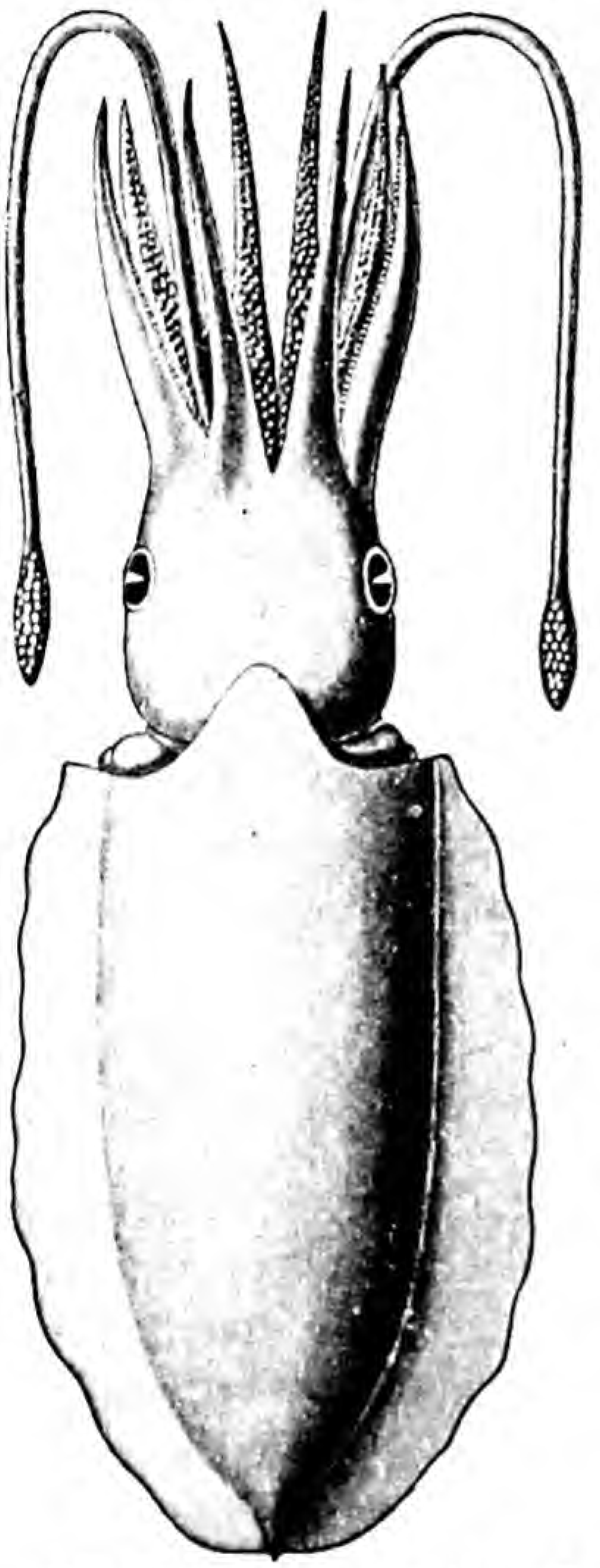


FIG. 613.—**Sepia cultrata.** Entire animal viewed from the antero-dorsal aspect.

The aperture of the mouth is surrounded by the bases of the ten *arms*. These are in pairs, situated to the right and left of the median plane. All of them, with the exception of the fourth pair (the most anteriorly situated pair being reckoned as the first), are stout at the base and taper towards the extremity. When extended they are about two-thirds of the length of the body. The outer surface of each (*i.e.*, that turned away from the mouth) is strongly convex, the inner flat, and beset throughout its length with a number of *suckers*, which are arranged in four longitudinal rows. Each sucker is in the form of a shallow cup, supported on a short, thick stalk; the lip of the cup is membranous, and immediately within it is a narrow, horny rim. Into the floor and walls of the cup are inserted numerous muscular fibres. When the sucker is being brought

into use it is firmly applied to the surface of the object; by the contraction of the muscular fibres the cavity of the cup is then enlarged, and a partial vacuum is formed, the result being firm adhesion, owing to the pressure of the surrounding water. The fourth pair of arms, usually known as the *tentacles*, are comparatively long and narrow, and provided with suckers only towards their free ends, which are somewhat thickened and club-like. In the male the fifth arm on the left side presents a slight modification, some of the suckers being absent. This is an indication of a change termed *hectocotylization*, which, as will be pointed out in the general account of the class, assumes in some cases a very remarkable character. As the nerves which supply them are derived from the pedal ganglia, it is assumed that the arms of Sepia represent a portion of the foot of other Molluscs; but there is some doubt as to whether they correspond to the forefoot or to the epipodia of the Gastropoda. The head-region, comprising as it does the arms (which, according to this assumption, are the chief part of the foot) and the head proper, is termed the *cephalopodium*. It has been pointed out, however, that for a number of reasons the arms should not be described as modified parts of the foot, but as appendages of the head. Only the funnel or siphon should, according to this view, be regarded to represent the molluscan foot, and the name *Siphonopoda* should therefore be adopted in place of the name Cephalopoda. The arguments for and against these opposing points of view are of a highly theoretical nature, and, for this reason, the older and more generally adopted interpretation has here been retained.

The trunk is covered over by the thick integument of the *mantle*, which terminates toward the oral end in a ridge round the neck. Anteriorly this ridge projects as a prominent rounded lobe under cover of which the head can be partially retracted. Posteriorly it forms the oral lip of the opening of a large cavity bounded by the mantle—the *mantle-cavity*—which extends along the entire posterior face of the body almost to the apex. The wide cleft between the oral edge of the mantle and the posterior surface of the body is not the only aperture leading into the mantle-cavity. On the oral side of this cleft is a large tube—the *funnel* (Fig. 614, *inf.*)—opening on the exterior behind the neck, and internally communicating by a wide aperture with the mantle-cavity. The cleft is capable of being almost completely closed by the apposition of a pair of oval projections (*mant. cart.*) of the inner surface of the posterior mantle-wall near its oral border, and a pair of concave depressions (*inf. cart.*) on the opposite (posterior) face of the funnel. The funnel is thus, under ordinary circumstances, the main outlet of the mantle-cavity. As such it not only carries to the exterior the effete water of respiration, the fæcal matters from the intestine, and the products of the excretory and reproductive organs, but also takes an important part in locomotion. The most important movements of the Cuttle-fish—by which it darts rapidly through the water in the direction

of the aboral pointed end of the body—are effected by the rhythmical contractions of the muscular walls of the mantle-cavity causing jets of water to be forced in the oral direction through the funnel. The free passage of water inwards through the funnel is prevented by the presence in its interior of a

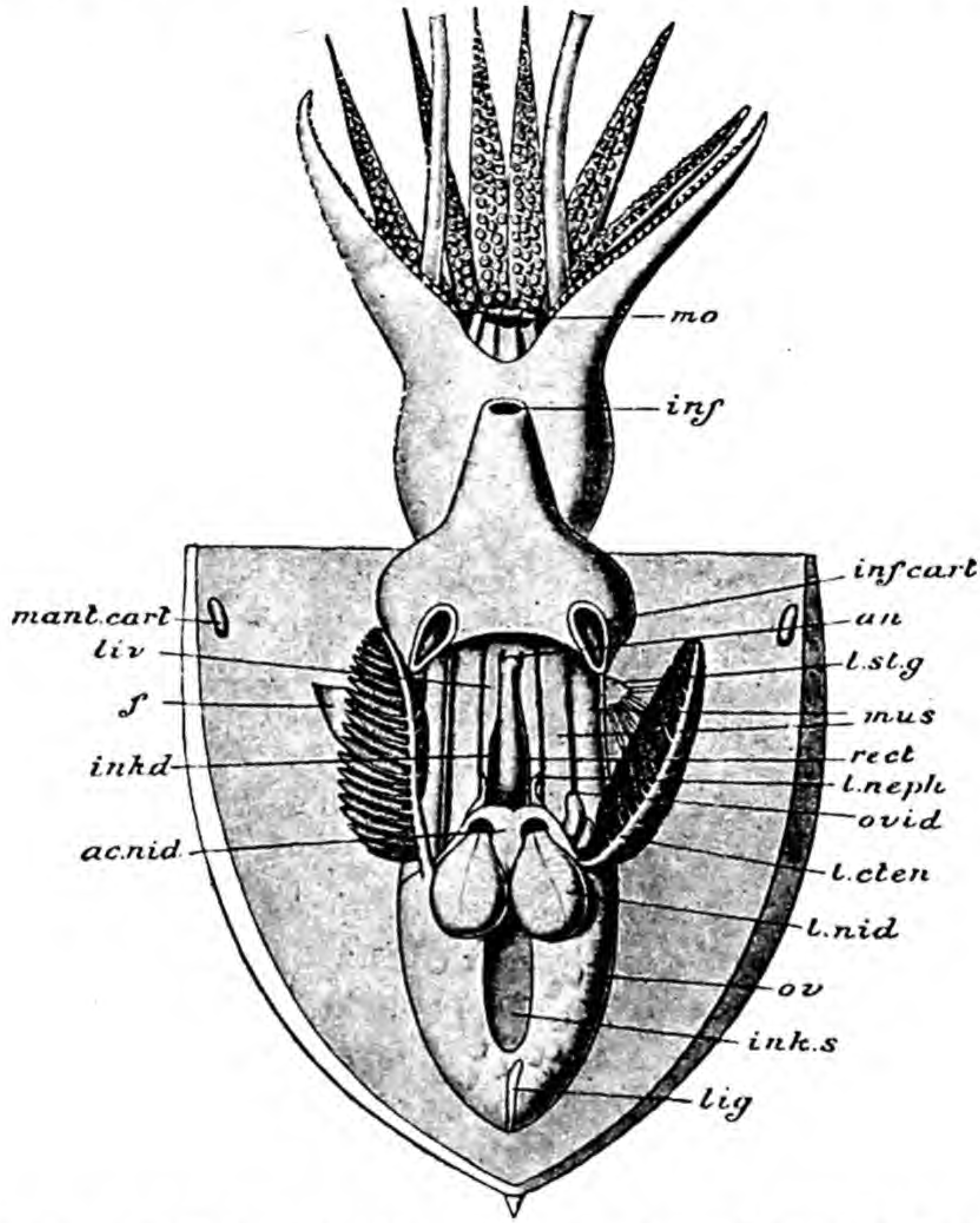


FIG. 614.—**Sepia cultrata,** female seen from the postero-ventral aspect, the wall of the mantle-cavity divided along the middle line and the two flaps thus formed spread out so as to expose the contents. *ac. nid.* accessory nidamental glands; *an.* anal aperture with its lateral appendages; *f.* membranous fold attaching the ctenidium to the wall of the mantle-cavity; *inf.* external opening of funnel; *inf. cart.* infundibular cartilage; *ink. d.* ink-duct; *ink. s.* ink-sac; *lig.* ligamentous band which extends from the anterior wall of the mantle-cavity to the ovary, cut across; *liv.* "liver"; *l. cten.* left ctenidium; *l. neph.* left renal aperture; *l. nid.* left nidamental gland; *l. st. g.* left stellate ganglion; *mant. cart.* mantle-cartilage; *mo.* mouth; *mus.* neck-muscles; *ov.* ovary; *ovid.* oviduct; *rect.* rectum.

flap-like valve opening outwards. The water required for respiration and in locomotion is thus drawn in, not through the funnel, but through the partially-closed slit-like pallial aperture previously referred to. The funnel seems, from the source of the nerves which supply it, to be, like the arms, a specially modified part of the foot.

Fringing each lateral margin of the body is a thin muscular fold—the *fin*—which is used as a swimming organ.

The anterior wall of the body exhibits, as already mentioned, a hard and resistant character owing to the presence of the internal **shell** (Fig. 615). This is completely enclosed in a sac of the mantle. Like the body itself, it is bilaterally symmetrical. In shape it may be described as leaf-like, with a rounded and comparatively broad oral end, and a narrower aboral end, provided with a sharp, anteriorly-projecting *spine*. The posterior surface is convex; the anterior convex towards its oral end, but deeply concave aborally, and bounded laterally by thin prominent wing-like ridges which converge to meet at the aboral extremity. The main mass of the shell consists of numerous, closely-arranged, thin laminæ of calcareous composition,

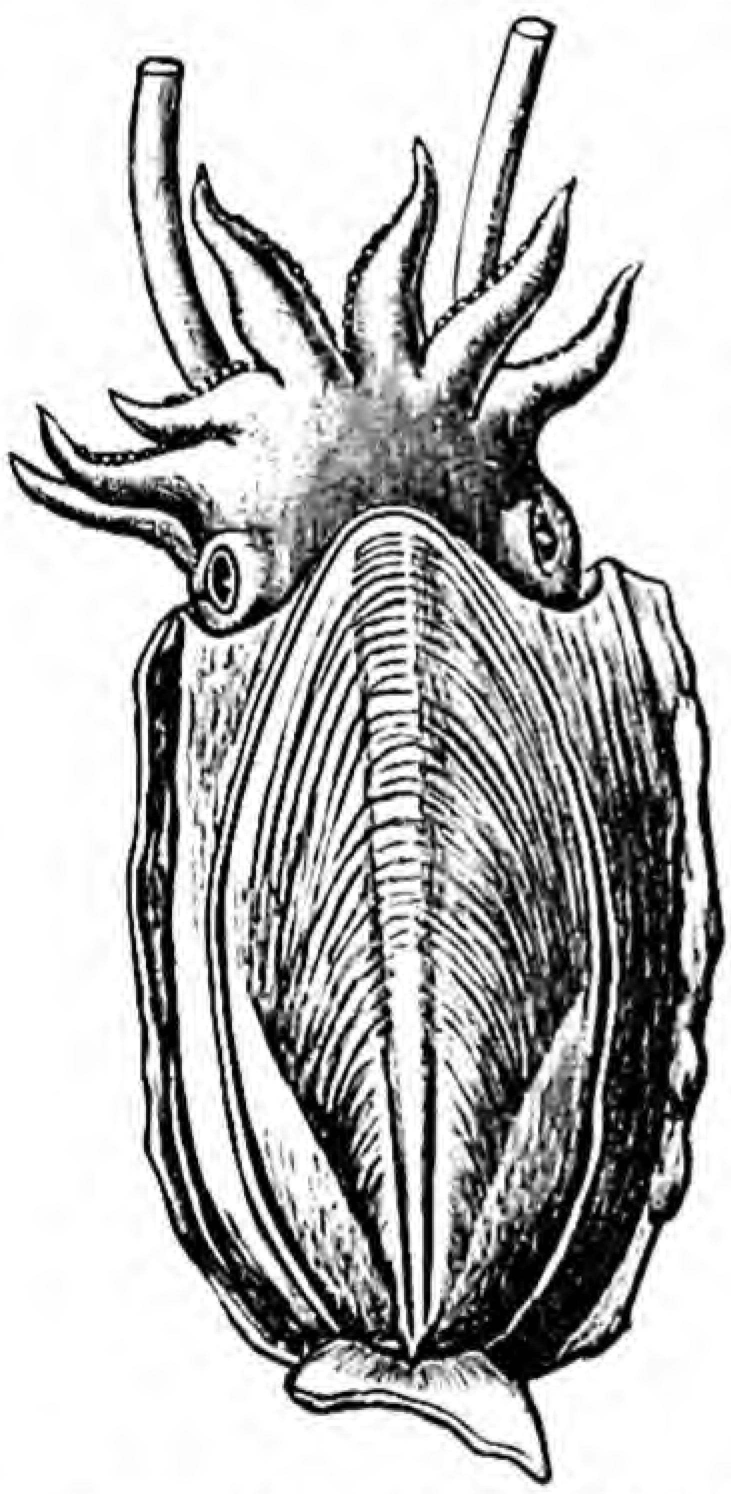


FIG. 615.—**Sepia officinalis** with mantle cut away to show the internal shell. (From *The Cambridge Natural History* (Macmillan & Co., Ltd.).)

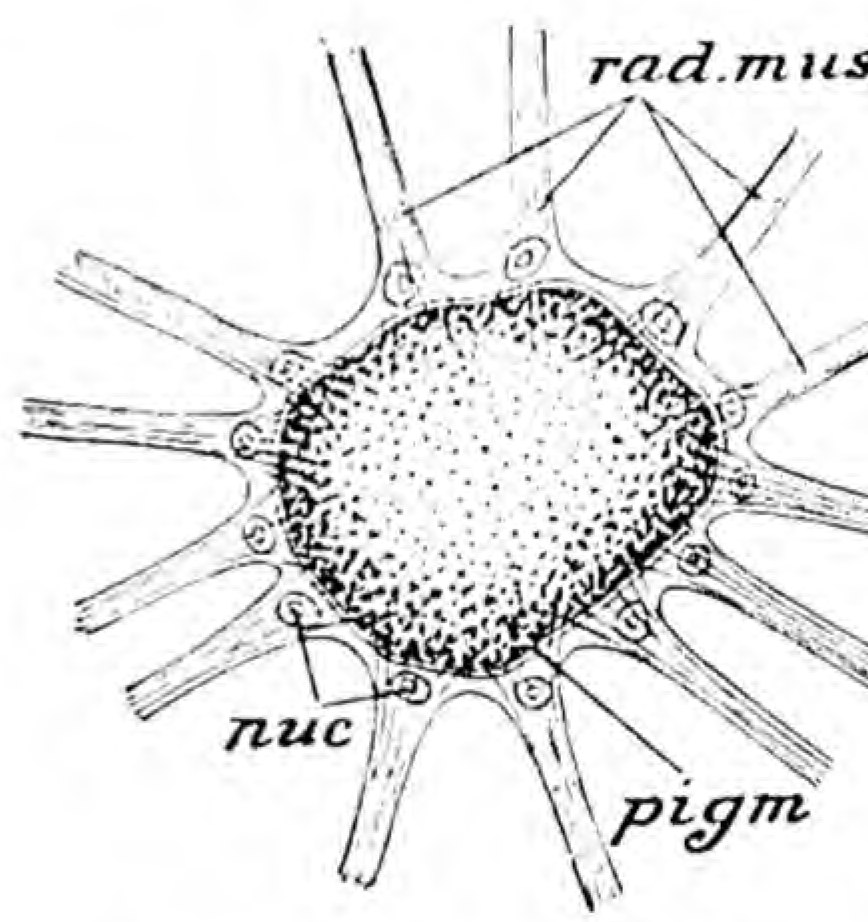


FIG. 616.—Chromatophore of **Sepia**, magnified. *nuc.* nuclei in wall of sac; *pigm.* pigment; *rad. mus.* radiating strands of muscle. (After Vogt and Jung.)

between which are interspaces containing gas. On the surface is a thin layer of chitinoid material, and slightly thicker strips of similar composition run along the margins.

The living Cuttle-fish will be observed to undergo frequent changes of colour, and blushes of different hues are to be observed passing over the surface. These are due to the presence of numerous contractile pigment-containing cells or **chromatophores** (Fig. 616) situated in the deeper layers of the integument over the entire surface. The chromatophores are flattened sacs with elastic walls, the contracting tendency of which is capable of being counteracted by the actions of bundles of muscular fibres radiating outwards from the edge of the sac into the surrounding tissues. When these radiating fibres are in action the

edge of the chromatophore is drawn outwards in different directions, and as a result the flattened sac becomes more expanded and thinner, the pigment being spread out into a thinner layer. When the fibres are relaxed the elasticity of the wall comes into play, and the chromatophore contracts, the contained pigment resuming its former arrangement. A peculiar iridescence which, in addition to the play of colours, is recognizable in the integument of *Sepia* is due to the presence of a number of cells, the *iridocytes*.

When the **mantle-cavity** is laid open (Fig. 614) there is seen on each side of it one of the two plume-shaped *ctenidia* (*cten.*). In the middle line of the posterior surface, close to the internal opening of the funnel, is the *anal aperture* (*an.*), situated at the oral extremity of a longitudinal tube—the *rectum*. On either side of the rectum is a much narrower projecting tube with a terminal opening—the *excretory aperture* (*neph.*). On the left-hand side is the opening of the oviduct (*ovid.*) or sperm-duct as the case may be.

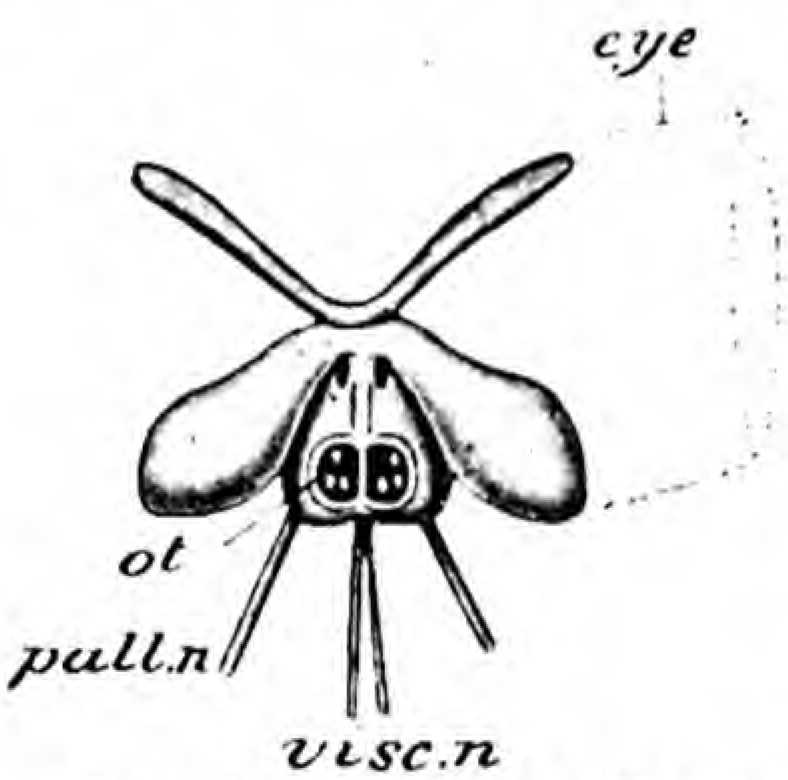


FIG. 617.—**Sepia cultrata,** cranial cartilage seen from the posterior aspect, with the cavities of the statocysts exposed. *eye*, position of eye indicated by dotted line; *ot*. statocyst; *pall. n*. pallial nerve; *visc. n*. visceral nerves.

In addition to the shell, which is an important protective structure, and gives support to the muscles of the fins, Sepia also has a remarkably well developed **internal skeleton** composed of cartilage. An important part of this—the *cranial cartilage* (Fig. 617)—protects the principal nerve-centres, encloses the statocysts, and gives support to the eyes. Other cartilages support the bases of the arms. A thin shield-shaped plate—the *nuchal* cartilage—lies on the posterior surface of the neck. The pair of elevations on the posterior wall of the funnel and the corresponding depressions on the anterior surface of the body are borne each on a thin plate of cartilage, and other thin cartilages support the bases of the fins.

Alimentary System.—The mouth is surrounded by a thin, lobed *peristomial membrane*, within which is a circular *lip* (Figs. 619, 622, *perist.*) beset with numerous papillæ. Lodged within the circular lip is a pair of powerful horny *jaws* (Fig. 618, Fig. 619, *jaw* 1, *jaw* 2; Fig. 620, *j.*; Fig. 622, *jaw*). These have somewhat the appearance of the beak of a parrot, the posterior jaw being larger and more strongly bent than the other, which it partly encloses. The mouth leads into a thick-walled buccal cavity, which contains an odontophore bearing numerous minute horny teeth. The *œsophagus* (Figs. 619 and 620, *œ*; Fig. 622, *œs*), following on the buccal cavity, is a narrow straight tube, which runs between the halves of the " liver " towards the aboral end of the body. It opens into a rounded thick-walled stomach (*st.*), and, close to the pyloric aperture leading from the latter into the intestine, opens a wide *cæcum* (*c.*).

The alimentary canal at this point bends sharply round upon itself, and the intestine runs nearly parallel with the œsophagus to open into the mantle-cavity as already described.

A pair of glands (Fig. 620, *s.g.*; Fig. 622, *sal.*), which are commonly termed *salivary*, though their functional correspondence with salivary glands has not been proved, are situated in the head behind the cranial cartilage. The ducts of these two glands run inwards and unite to form a median duct, which opens

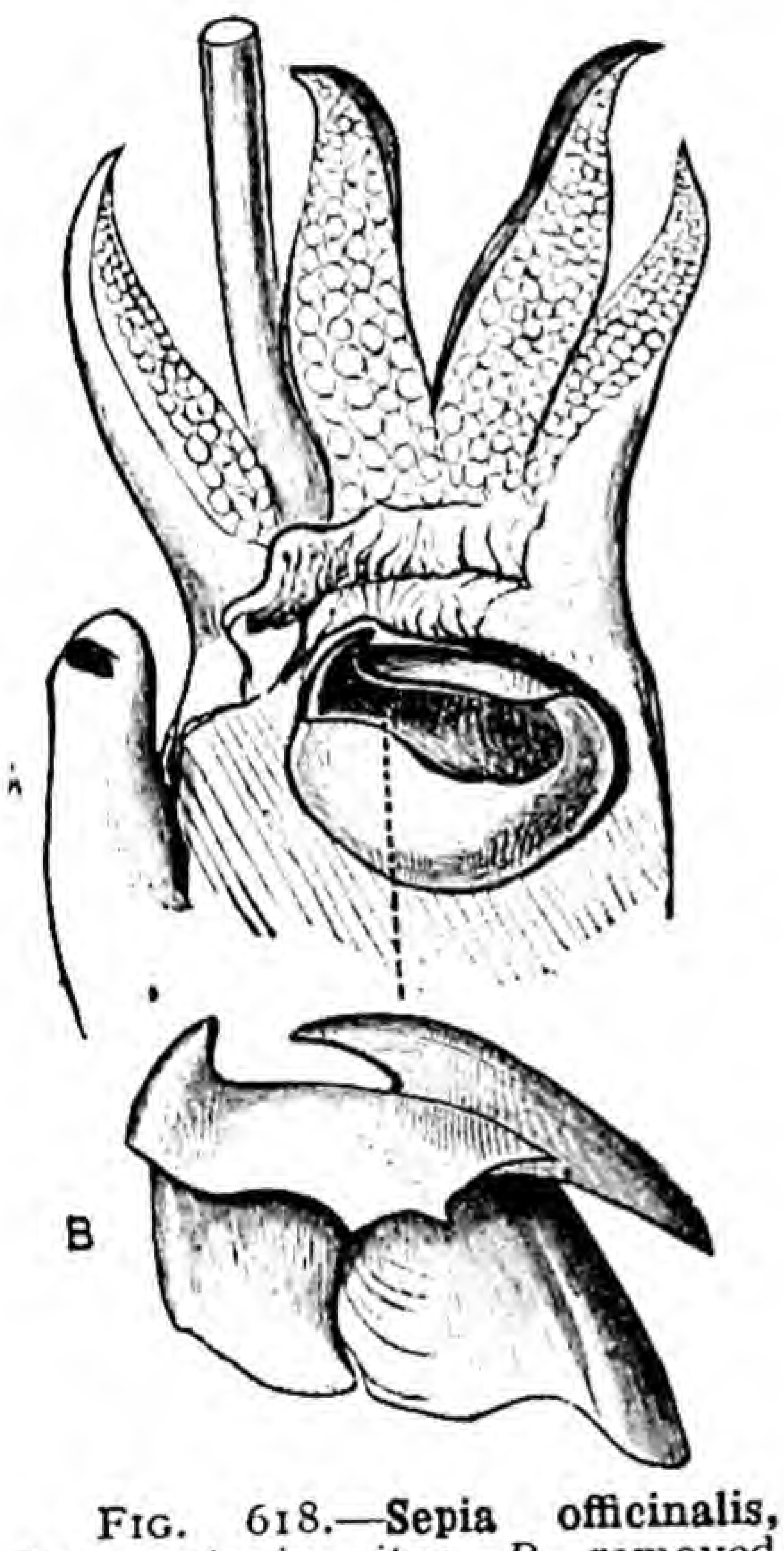


FIG. 618.—**Sepia officinalis,** jaws. *A, in situ*; *B*, removed and slightly enlarged. (From the *Cambridge Natural History*.)

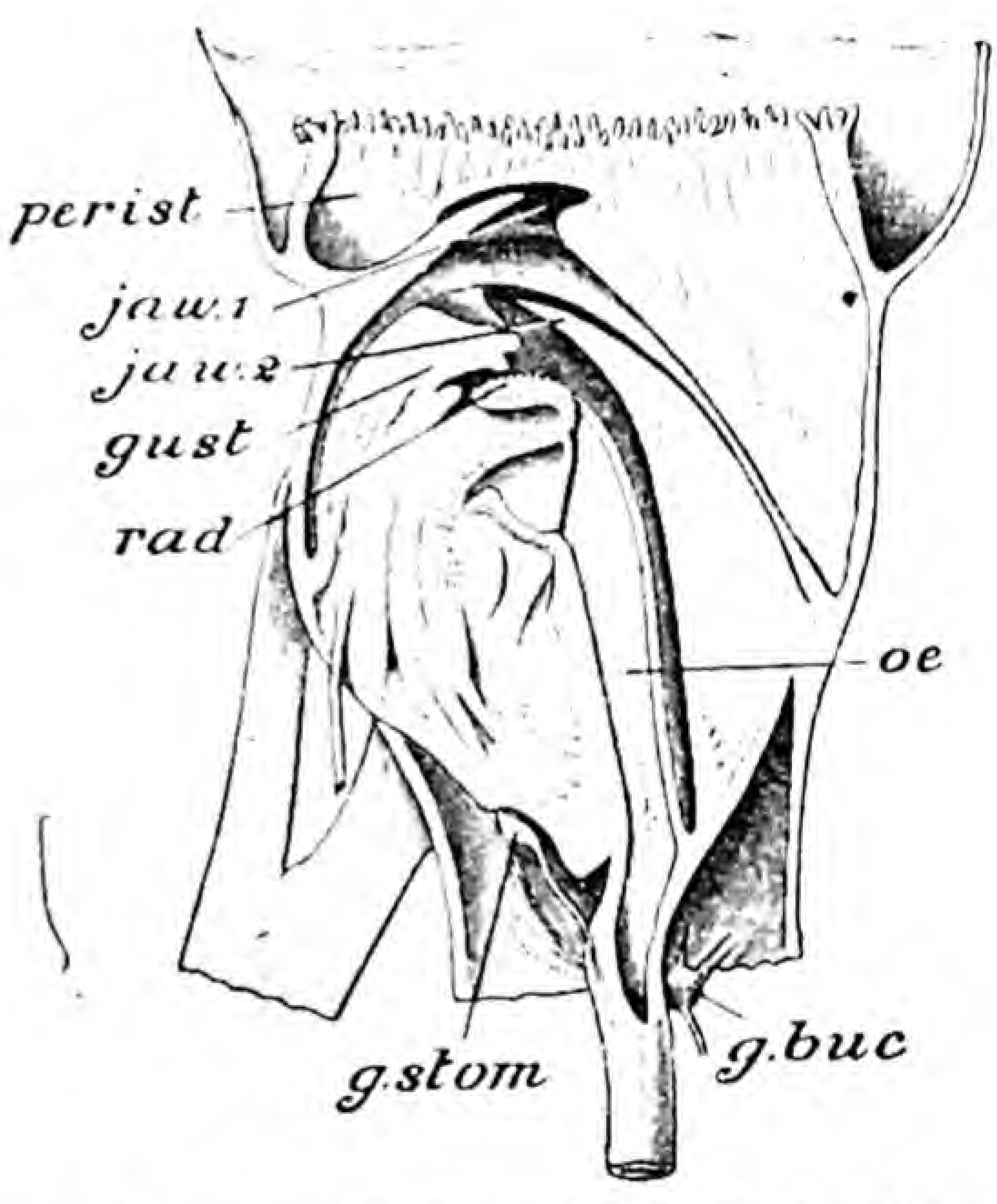


FIG. 619.—**Sepia,** median section through the buccal mass. *g. buc.* superior buccal ganglia; *g. stom.* inferior buccal ganglia; *gust.* supposed gustatory organ; *jaw 1*, posterior jaw; *jaw 2*, anterior jaw; *œ.* œsophagus; *perist.* circular lip; *rad.* radula. (After Keferstein.)

into the buccal cavity. The name of "*liver*" (Fig. 620, *l, l.*; Fig. 621, *liv.*) or *digestive gland* is given to a large brown glandular mass which extends from the neighbourhood of the salivary glands nearly to the aboral end of the body. It consists of two partly united right and left portions, each of which has a duct opening into the cavity of the alimentary canal opposite the point where stomach, cæcum, and intestine meet. Surrounding the ducts and opening into them are masses of minute vesicles (Fig. 620, *b, d.*); the secretion of these has the property of converting starchy matters into sugar; they receive the name of *pancreas*.

Immediately below the thin integument of the anterior wall of the mantle-cavity lies a characteristic organ—the **ink-sac** (Fig. 614, *ink. s.*; Fig. 620, *i.*). This is a pear-shaped body, a portion of the interior of which is glandular and secretes a black substance—the *ink* or *sepia*—which collects in the main cavity of the sac and is discharged by a cylindrical duct opening to the rectum close to the anal aperture. When the Cuttle-fish is startled it discharges the ink which, mixing with the water in the mantle-cavity, is ejected through the funnel as a black cloud, under cover of which the animal may escape from a threatened attack.

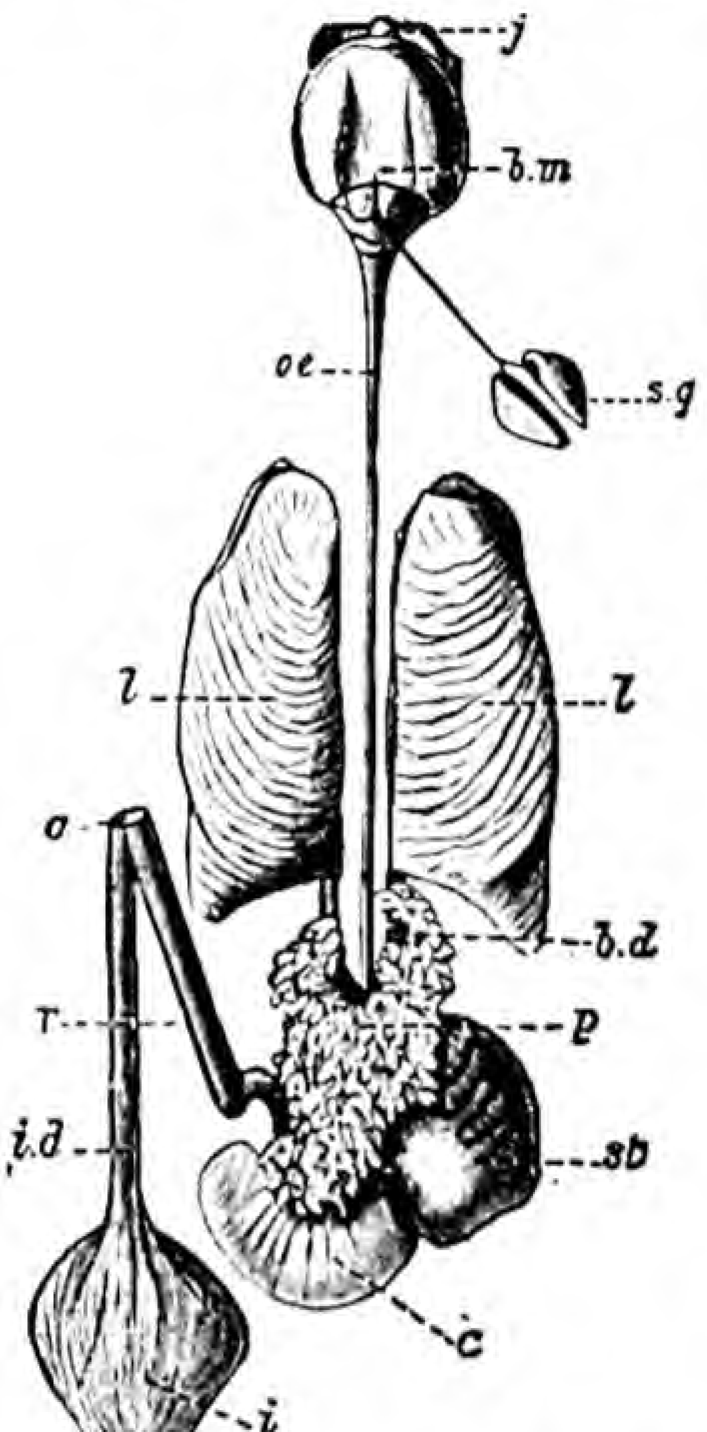


FIG. 620.—**Sepia officinalis,** enteric canal. *a.* anus; *b. d.* duct of one of the portions of the digestive gland; *b. m.* buccal mass; *c.* cæcum; *i.* ink-sac; *i. d.* ink-duct; *j.* jaws; *l. l.* digestive gland; *œ.* œsophagus; *p.* pancreatic appendages; *r.* rectum; *s. g.* salivary glands; *st.* stomach. (From the *Cambridge Natural History*.)

Vascular System.—The *heart* (Figs. 621, 622, and 624) of the Cuttle-fish consists of a ventricle and two auricles. The *ventricle* (*vent.*), which is divided into two lobes by a constriction, is somewhat obliquely placed, but the rest of the vascular system is almost completely equilateral. At its oral end the ventricle gives off a large vessel—the *oral aorta* (Fig. 624, *aort.*); aborally it gives origin to a much smaller *aboral aorta* (*aort'.*), which bends over the ink-sac and supplies the aboral portions of the body. The arteries which lead off from the aortæ communicate by their ultimate branches with a system of capillaries, and these with a system of veins. A large median vein, the *vena cava* (*v. cav.*), runs from the head to the neighbourhood of the rectum, in front of which it bifurcates to form the left and right afferent branchial veins (*l. aff. br. v., r. aff. br. v.*), each running through the cavity of the corresponding renal organ to the base of the gill, where it is joined by veins from the aboral region. At the base of the gill the afferent branchial vein becomes dilated to form a contractile sac—the *branchial heart* (*r. br. ht.*)—appended to which is a rounded body of a glandular character—the *appendage* of the branchial heart, representing the pericardial glands of the Bivalvia. The afferent branchial vein runs through the axis of the branchia, giving off branches as it goes. The blood is carried back to the ventricle on either side by a dilated contractile vessel, the ***auricle*** or *efferent branchial vein* (*l. aur., r. aur.*).

The **cœlome** (Fig. 628) is a pouch of considerable size, divided by a constriction into oral and aboral parts. The former is the *pericardium*, or cavity in which the heart is lodged; it gives off a pair of diverticula, right and left, each lodging the corresponding branchial heart, and communicates by a pair of

apertures with the cavities of the kidneys or renal sacs. The aboral part of the cœlome forms the capsule (*gonocœle*) which encloses the ovary or testis.

The paired, plume-shaped **ctenidium** lies parallel with the long axis of the body. It is attached throughout the greater part of its length to the wall of

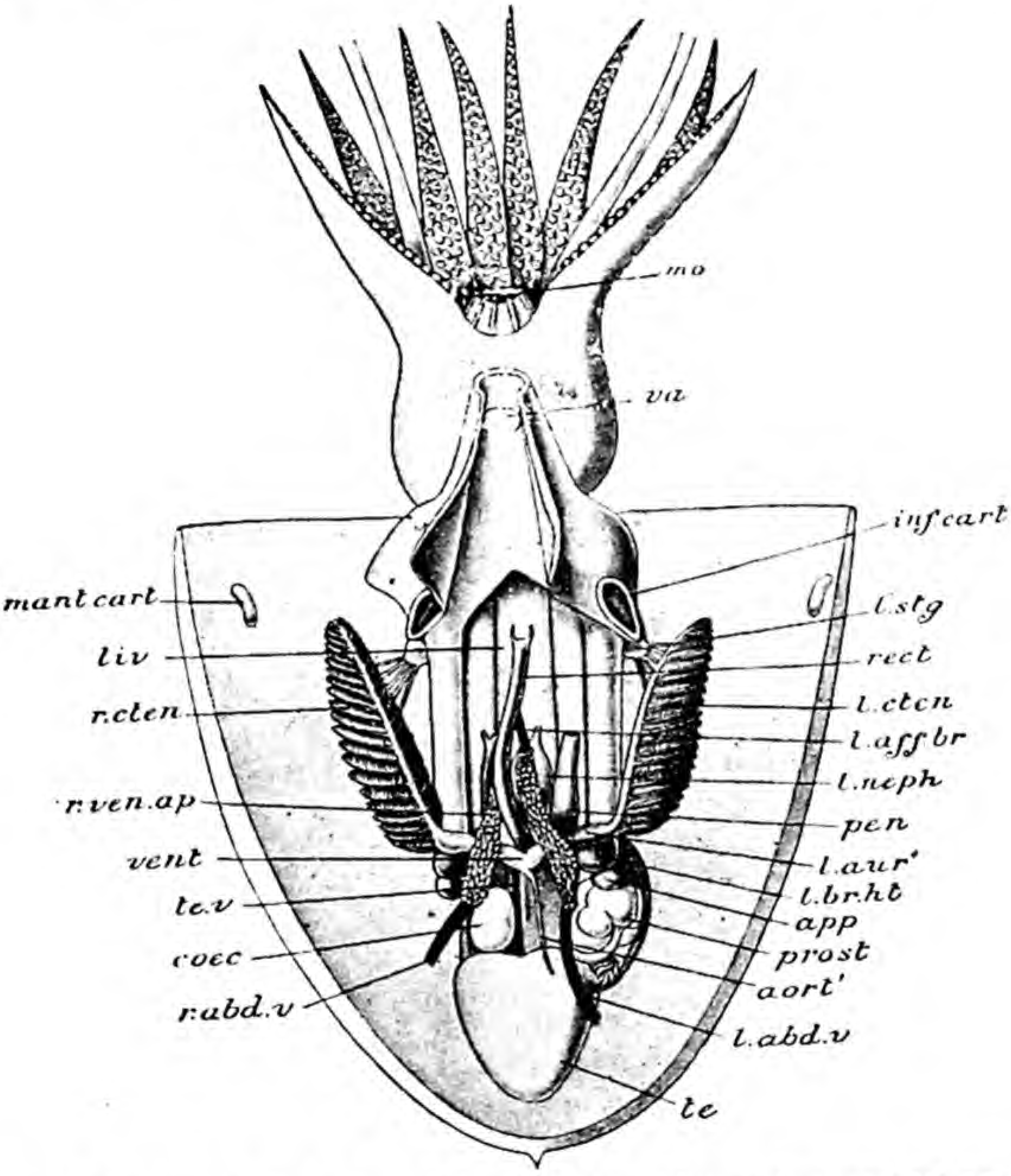


FIG. 621.—**Sepia cultrata,** male specimen seen from the postero-ventral aspect, the mantle-cavity opened as in Fig. 614, the posterior body-wall partly dissected off, so as to expose the organs in the visceral sac; the ink-sac and duct removed. *aort'.* aboral aorta; *app.* appendage of left branchial heart; *cœc.* cæcum; *inf. cart.* funnel cartilages; *liv.* digestive gland; *l. abd. v.* left abdominal vein; *l. aff. br.* left afferent branchial vessel; *l. aur.* left auricle; *l. br. ht.* left branchial heart; *l. cten.* left ctenidium; *l. neph.* left kidney; *l. st. g.* left stellate ganglion; *mant. cart.* mantle-cartilage; *mo.* mouth surrounded by peristomial membrane; *pen.* penis; *prost.* prostate; *r. abd. v.* right abdominal vein; *r. cten.* right ctenidium; *rect.* rectum; *r. ven. ap.* appendages of right afferent branchial vessel; *te.* testis; *te. v.* vein to testis; *va.* valve of funnel; *vent.* ventricle.

the mantle-cavity by a thin muscular fold, and consists of numerous pairs of delicate lamellæ, the surface of which is increased by the presence of a complex system of foldings. Internally the lamellæ are not completely in contact, an axial canal being left through which the water penetrates freely to all parts of the gill. The blood carried to the gill by the afferent branchial vessel passes

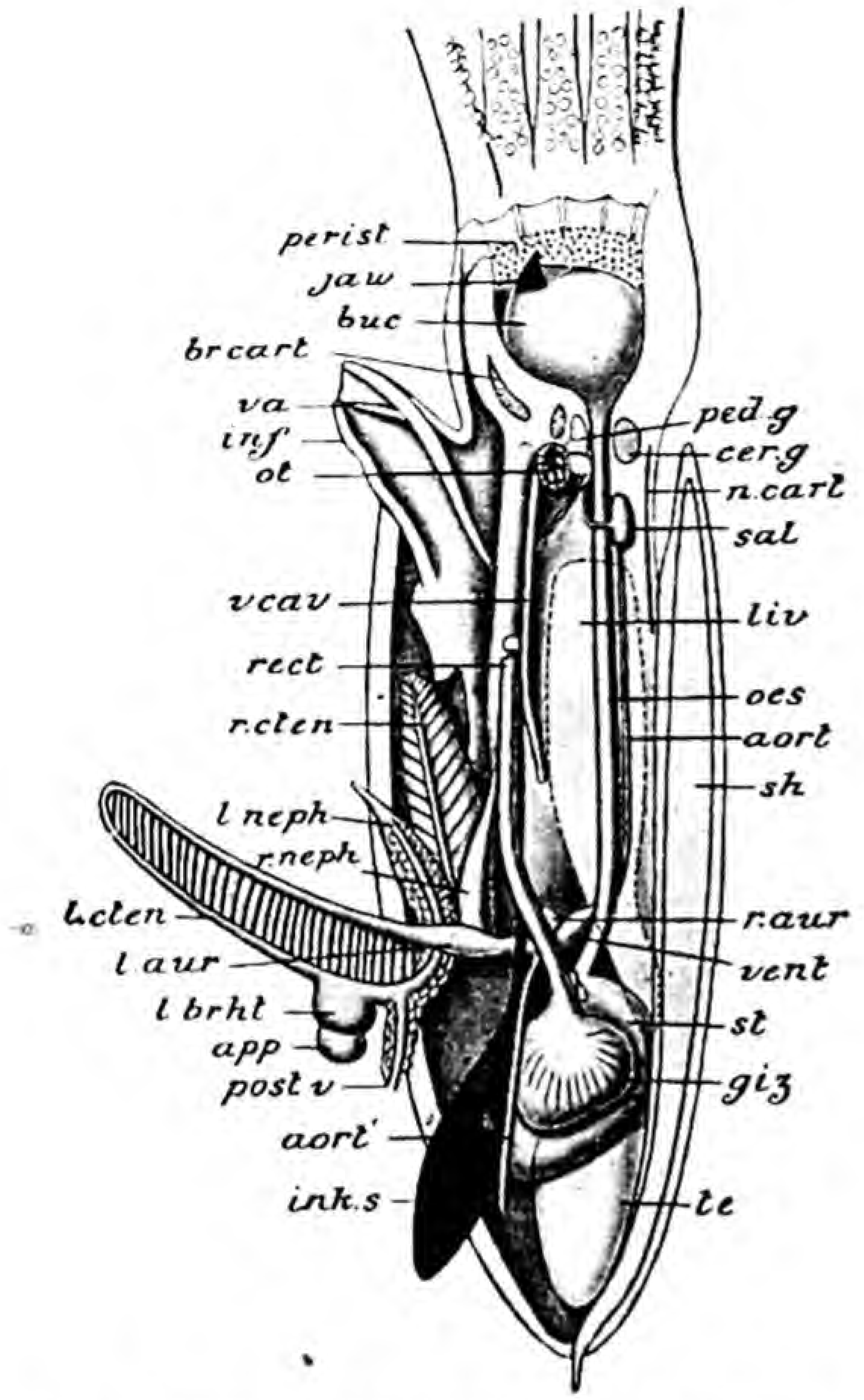


FIG. 622.—**Sepia cultrata,** lateral dissection of male. The left-hand half of the head has been removed by an approximately median longitudinal section, the buccal mass, however, being left intact; the funnel and the anterior and posterior walls of the mantle-cavity are likewise bisected longitudinally. The left ctenidium with the left renal sac and left branchial heart have been removed from their natural position and displaced backwards so as to expose the other organs. The digestive gland with its ducts and the pancreatic appendages have been removed, but the position of the former is indicated by a dotted line. *app.* appendage of left branchial heart; *aort.* aorta; *aort'.* aboral aorta; *buc.* buccal mass; *br. cart.* section of cartilage supporting the arms; *cer. g.* cerebral ganglia; *giz.* cæcum; *ink. s.* ink-sac; *inf.* funnel; *jaw.* jaw; *l. aur.* left auricle; *l. br. ht.* left branchial heart; *l. cten.* left ctenidium; *liv.* position of digestive gland; *l. neph.* left renal sac; *n. cart.* nuchal cartilage; *œs.* œsophagus; *ot.* cavity of statocyst laid open; *ped. g.* section of pedal ganglion; *perist.* points to circular lip with peristomial membrane surrounding it; *post. v.* abdominal vein; *r. aur.* right auricle; *r. cten.* right ctenidium; *rect.* rectum; *sal.* salivary gland; *sh.* shell; *st.* stomach; *te.* testis; *va.* valve of funnel; *v. cav.* vena cava; *vent.* ventricle.

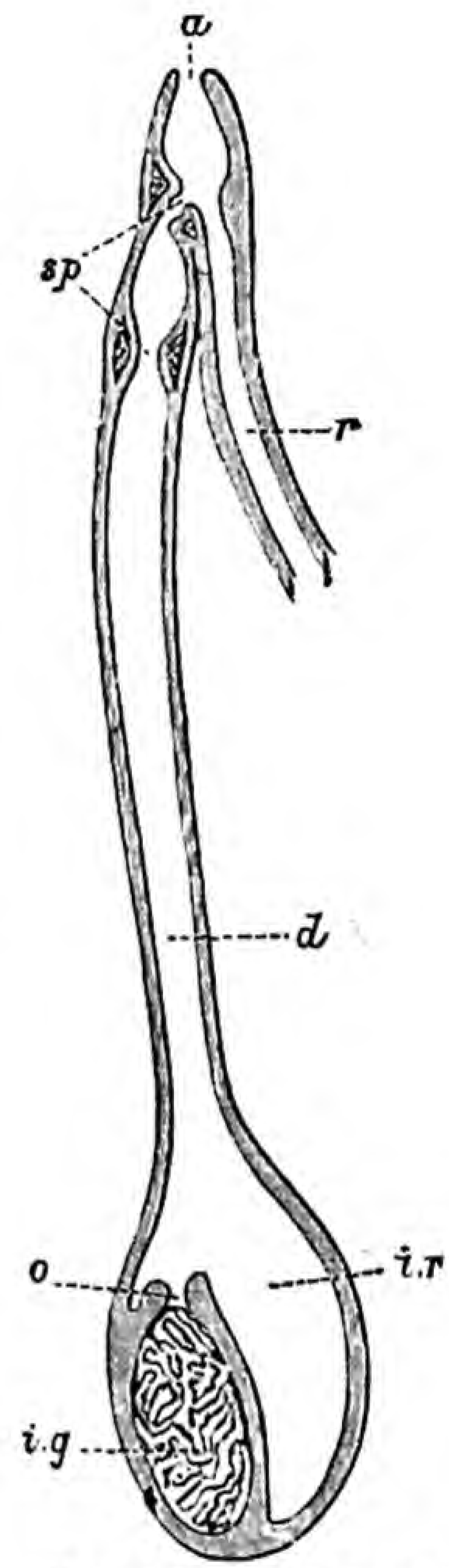


FIG. 623.—**Sepia officinalis,** longitudinal section of ink-sac. *a.* anus; *d.* ink-duct; *i. g.* ink-gland; *i. r.* cavity of ink-sac; *o.* orifice of ink-gland; *r.* rectum; *sp.* sphincter muscles. (From the *Cambridge Natural History,* after Girod.)

in a system of minute branches through the lamellæ, and is gathered up again into vessels which open into the main efferent vessel leading to the auricle.

Nervous system.—Though parts homologous with those of Triton are recognizable in the nervous system of Sepia, their proportions and arrangement indicate a higher grade of organization. The *cerebral, pedal,* and *pleuro-visceral ganglia*, all of relatively large size, are closely aggregated together around the œsophagus, supported and protected by the cranial cartilage. The *cerebral ganglia* (Fig. 625, *Cg.*) are fused together into a rounded mass, lodged in a hollow of the cranial cartilage, and covered over anteriorly by a strong

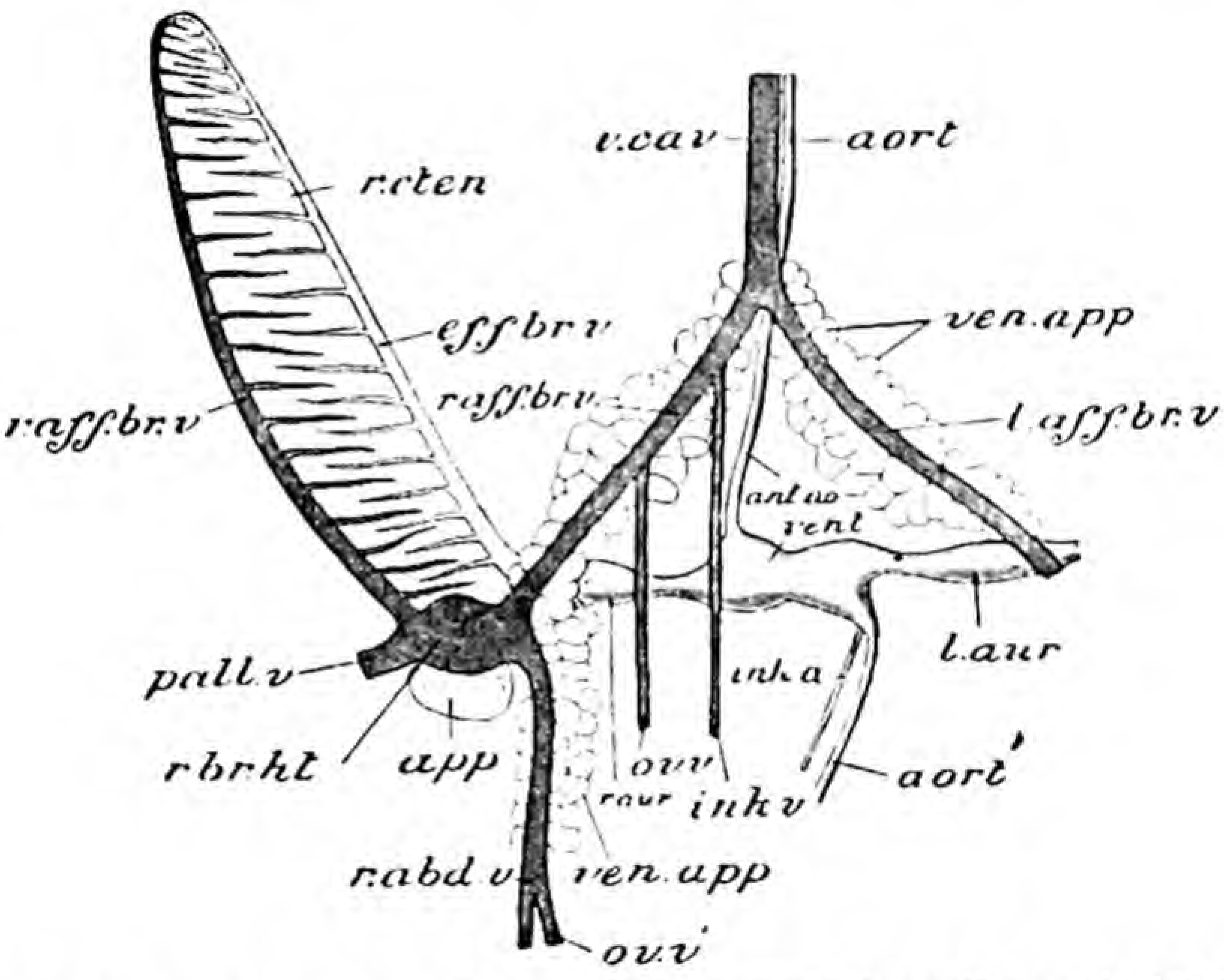


FIG. 624.—**Sepia cultrata,** heart and main blood-vessels from the posterior aspect. *ant. ao, aort.* aorta; *aort'.* aboral aorta; *app.* appendage of right branchial heart; *eff. br. v.* right efferent branchial vessel; *ink. a.* artery to ink-sac; *ink. v.* vein from ink-sac; *l. aff. br. v.* left afferent branchial vessel; *l. aur.* left auricle; *ov. v.* deep ovarian vein; *ov. v'.* superficial ovarian vein; *pall. v.* pallial vein; *r. abd. v.* right abdominal vein; *r. aff. br. v.* right afferent branchial vein; *r. cten.* right ctenidium; *r. br. ht.* right branchial heart; *v. cav.* vena cava; *ven. app.* venous appendages; *vent.* ventricle.

fibrous membrane. Laterally are given off a pair of short thick processes—the *optic nerves* or *optic stalks*—which expand almost immediately into large masses—the *optic ganglia* (*Go.*)—in immediate contact with the eyes. At the sides and posteriorly a pair of very thick commissural bands of nerve-matter pass round the œsophagus to unite with the pedal and pleuro-visceral ganglia, which lie behind. The *pedal ganglia* are, like the cerebral, united into a single mass; orally this is prolonged and expanded into a broad mass from which the ten *brachial nerves* (*Bn.*) are given off to the arms. The *pleuro-visceral* ganglia (*Vg.*), also united into one, are in immediate contact with the pedal behind the œsophagus.

Besides the optic nerves the cerebral ganglia also give off a pair of slender nerves which join a smaller pair of closely united superior *buccal* ganglia (Fig. 625, *Bc.*), situated close to the buccal mass on the anterior aspect of the œsophagus. The buccal ganglia again (which are sometimes looked upon as separated portions of the cerebral) are connected by slender connectives with a pair of inferior buccal ganglia (Fig. 619, *g. stom.*), also closely united, situated on the posterior aspect of the œsophagus. Besides the ten brachial nerves (Fig. 625, *Bn.*), each of which, expanding at the base of the arm into a *brachial ganglion* (*Bg.*), runs along the axis of the arm to its extremity, the pedal ganglia also give off nerves to the funnel, and also a pair to the statocysts; but the latter are found, when their fibres are traced to their origin, to be derived from the cerebral ganglia. The pleuro-visceral ganglia give off two *visceral nerves* (*Vn.*) supplying the various internal organs, one pair of branches, the *branchials* (*Brn.*), having each a branchial ganglion at the base of the ctenidium (*Gb.*), and running along its axis to its extremity. The pleuro-visceral ganglia also give off two very stout *pallial nerves* (*Pn.*) which run through the neck to the inner surface of the mantle-cavity, where each expands into a large, flat, *pallial* or *stellate* ganglion (*Gst.*), which is visible in front of the ctenidium when the mantle-cavity is opened. From the outer edge of this arise a number of nerves supplying the various parts of the mantle. A loop of *sympathetic nerves* (*Ns.*) arises from the inferior buccal ganglia and runs along the œsophagus to the stomach where it ends in the *gastric ganglion* (*Gg.*).

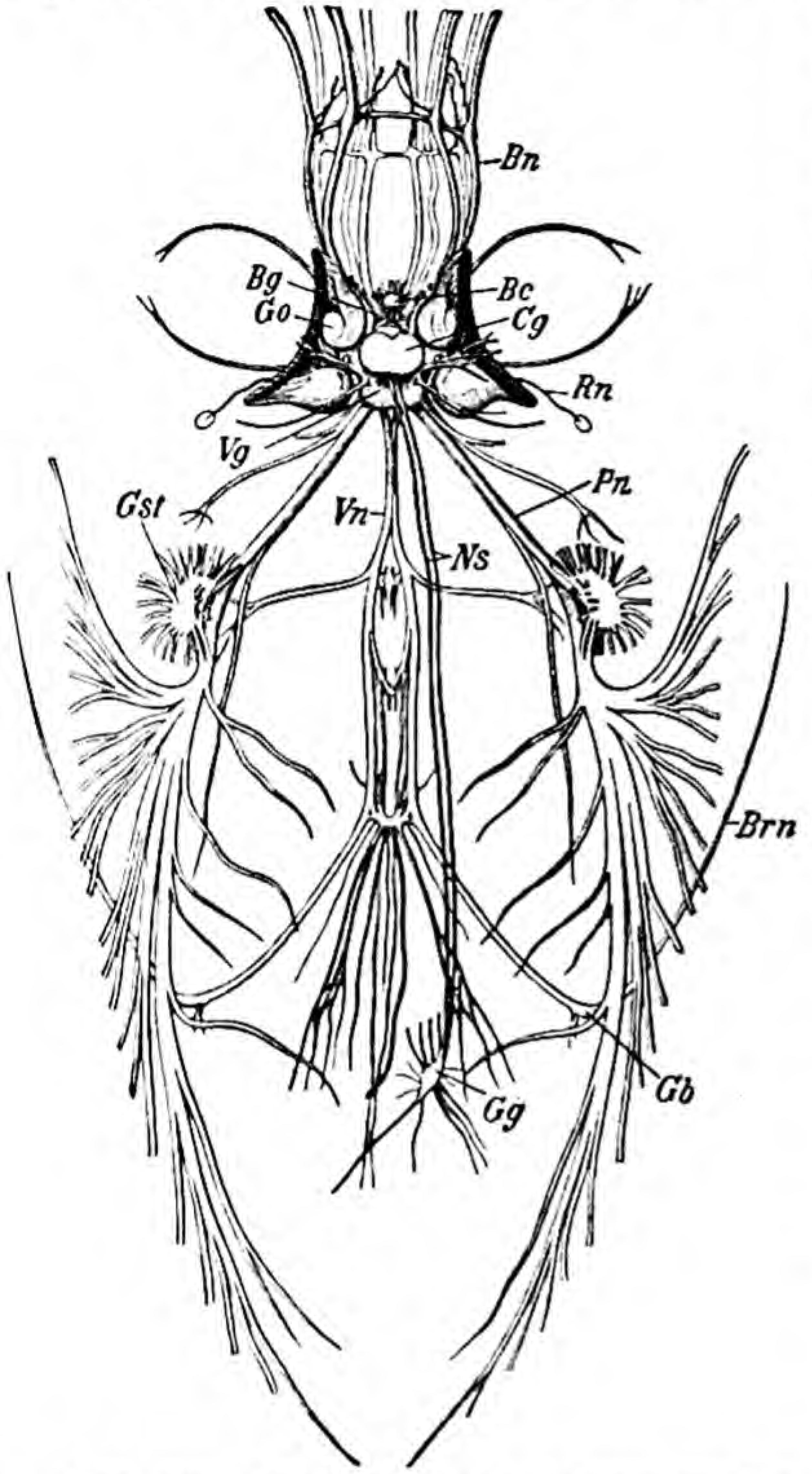


FIG. 625.—**Sepia officinalis,** nervous system. *Bc.* superior buccal ganglion; *Bg.* brachial ganglion; *Bn.* brachial nerves; *Brn.* branchial nerve; *Cg.* cerebral ganglion; *Gb.* branchial ganglion; *Gg.* gastric ganglion; *Go.* optic ganglion; *Gst.* stellate ganglion; *Ns.* sympathetic nerve; *Pn.* pallial nerve; *Rn.* olfactory nerve; *Vg.* pleuro-visceral ganglion; *Vn.* visceral nerves. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Hillig.)

The **sense-organs** of the Cuttle-fish are much more highly developed than those of Triton. The *eyes* (Fig. 626) are supported by curved plates of cartilage forming a sort of orbit, connected with the cranial cartilage. A transparent portion of the integument covering the exposed face of the eye is termed the *false cornea* (*corn*). The eyeball has a firm wall, or *sclerotic*, strengthened by plates of cartilage (*scl. cart.*). Externally, *i.e.*, on the side turned towards the surface of the head, this presents a large opening—the *pupil*. The part of the sclerotic which immediately bounds the pupil is termed the *iris* (*ir.*); it contains muscular fibres by whose action the size of the pupil can, to a limited

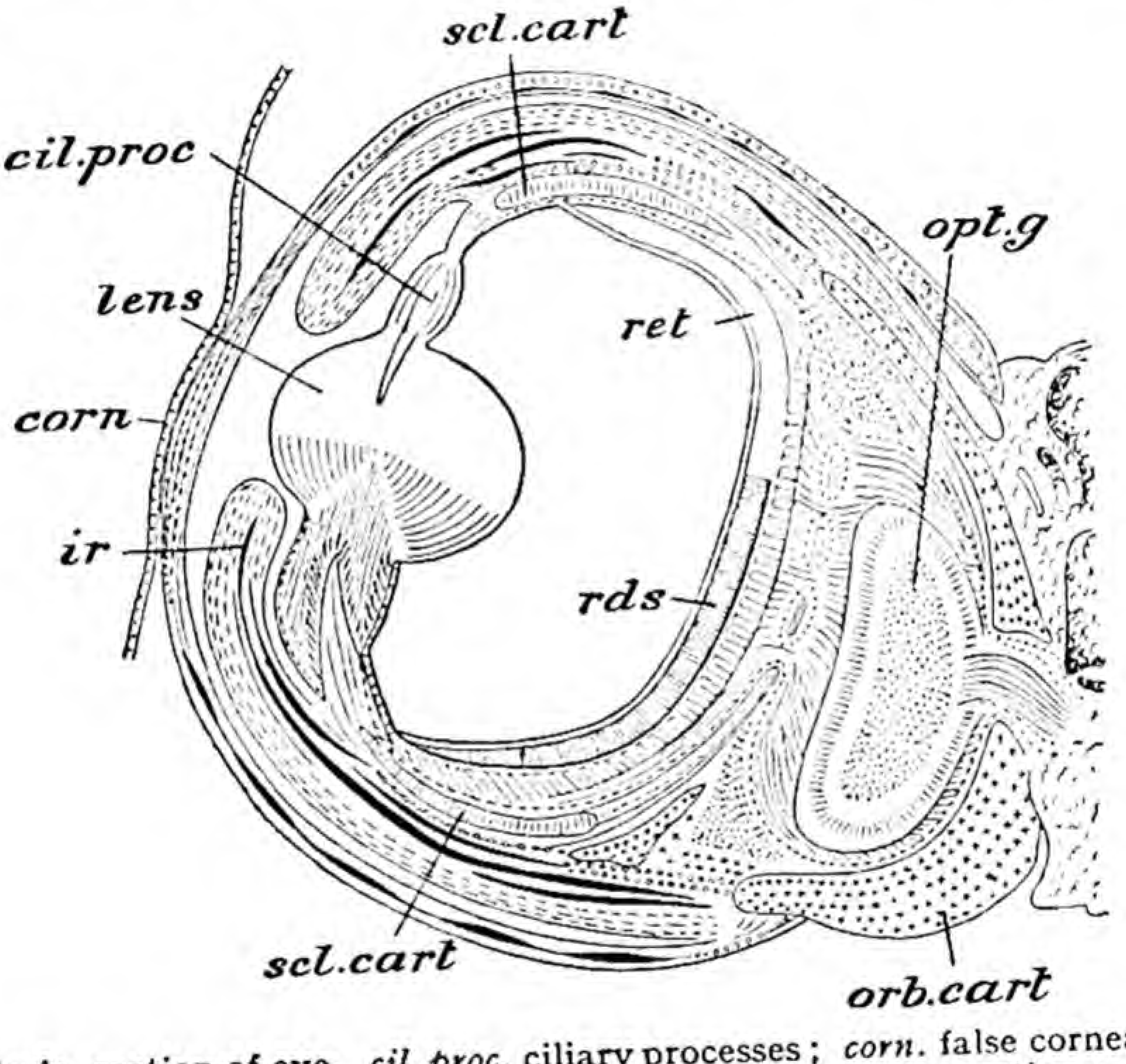


FIG. 626.—**Sepia,** section of eye. *cil. proc.* ciliary processes; *corn.* false cornea; *ir.* iris; *lens.* lens; *opt. g.* optic ganglion; *orb. cart.* orbital cartilage; *rds.* rods; *ret.* retina; *scl. cart.* sclerotic cartilage. (From Vogt and Jung, after Hensen.)

extent, be increased or diminished. Just internal to the iris and projecting slightly through the pupil is the *lens*—a dense glassy-looking body of a spherical shape. The lens consists of two plano-convex lenses in close apposition; it is supported by an annular process—the *ciliary process* (*cil. proc.*)—projecting inwards from the sclerotic. Between the two parts of the lens lies a thin layer of cells—the *cornea.* The lens with the ciliary process divides the cavity of the eye into two portions, a smaller outer—the cavity of the *aqueous humour*, containing water, and a larger inner, containing a gelatinous substance—the *vitreous humour.* Over the wall of this inner chamber extends the *retina* (*ret.*) the sensitive part of the eye, in which the optic nerve-fibres derived from the optic ganglion terminate. The retina is of somewhat complicated structure.

mainly composed of a layer of close-set parallel *rods* (*rds.*), which immediately bound the cavity of the eye, with externally a layer of *retinal cells* which are in communication with the rods internally and with the *optic nerve-fibres* externally.

In immediate contact with the eye, in addition to the optic ganglion, is a large soft body of unknown function, the so-called *optic gland* or *white body*. Bundles of muscular fibres bring about limited movements of the eyeball in various directions. An integumentary fold of the character of an eyelid is

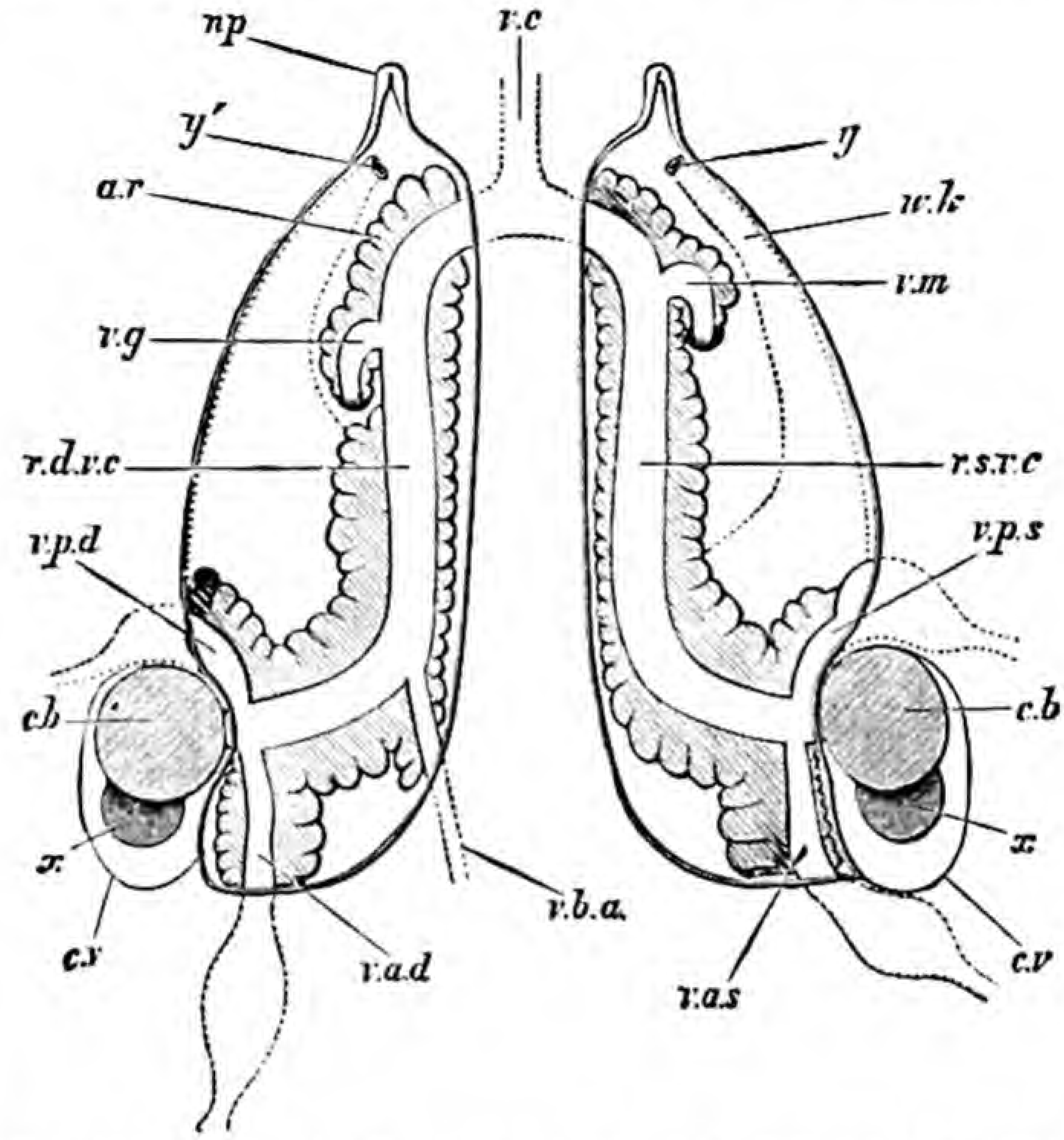


FIG. 627.—**Sepia officinalis**, excretory organs (ventral view, upper walls of renal sacs removed). ***a. r.*** glandular renal outgrowths; *c. b.* branchial heart; *c. v.* capsule of branchial heart; ***n. p.*** external aperture of right renal sac; ***r. d. v. c.*** right descending branch of vena cava; ***r. s. v. c.*** left descending branch of vena cava; ***v. a. d.*** right abdominal vein; ***v. a. s.*** left abdominal vein; *v. b. a.* vein from ink-sac; *v. c.* vena cava; ***v. g.*** genital vein; ***v. m.*** mesenteric vein; ***v. p. d.*** right pallial vein; *v. p. s.* left pallial vein; *w. k.* viscero-pericardial sac (dotted outline); *x.* appendage of the branchial heart; *y. y′.* left and right reno-pericardial orifices. (From Lankester's *A Treatise on Zoology* (Adam & Charles Black), after Vigelius.)

capable of being drawn to some extent over the false cornea. In many respects the eye of Sepia strikingly resembles the *vertebrate* eye.

The *statocyst*, though not of such complicated structure as the eye, is very much more highly developed than that of the Gastropoda or Bivalvia. The two statocysts are embedded in the cartilage of the posterior portion of the cranium close to the pleuro-visceral ganglion. The cavities of the two organs, which are about 3 mm. in diameter, are separated by a median cartilaginous septum. The inner surface presents a number of rounded and pear-shaped elevations, and is lined with a flattened epithelium raised up on the posterior surface into a ridge or *crista* statica and a *macula* statica composed of large

cylindrical cells provided at their free extremities with short hair-processes, and produced at their bases into processes continuous with nerve-fibres derived from the statocyst-nerve. Enclosed in the cavity of the statocyst and attached to the macula is a large statolith of dense composition and complicated form. It has been shown by experiment that the removal of the statocysts leads to a loss of the power of co-ordinating the movements in such a way as to maintain the equilibrium.

Supposed to be *olfactory* in function is a pair of ciliated pits, which open by slits on the surface behind each eye; among the ciliated cells lining the pit are numerous narrow sensory cells connected at their bases with the fibres of a nerve derived from a small ganglion situated close to the optic ganglion. A small elevation (Fig. 619, *gust*), covered with papillæ, on the floor of the buccal cavity just in front of the odontophore, is perhaps an *organ of taste*.

The **excretory organs** or **kidneys** of Sepia (Figs. 627 and 628) are a pair of thin-walled sacs, which open into the mantle-cavity by the conspicuous excretory apertures already described. On either side is an aperture (Fig. 627, *y*., *y'*.) placing the cavity of the sac in communication with the pericardium, and the right and left sacs communicate with one another orally and aborally. From their posterior junction is given off a median diverticulum (Fig. 628, *med. s.*), into which the pancreatic follicles (*panc.*) project. Through each excretory sac runs the corresponding *afferent branchialvein* (Fig. 627, *r. d. v. c.* and *l. d. v. c.*), formed by the bifurcation of the vena cava, and surrounding it are masses of glandular tissue (*a. r.*), by whose agency the process of renal excretion (the products of which, in the shape of a nitrogenous excretory substance called *guanin*, are to be detected in the internal cavity) is carried on.

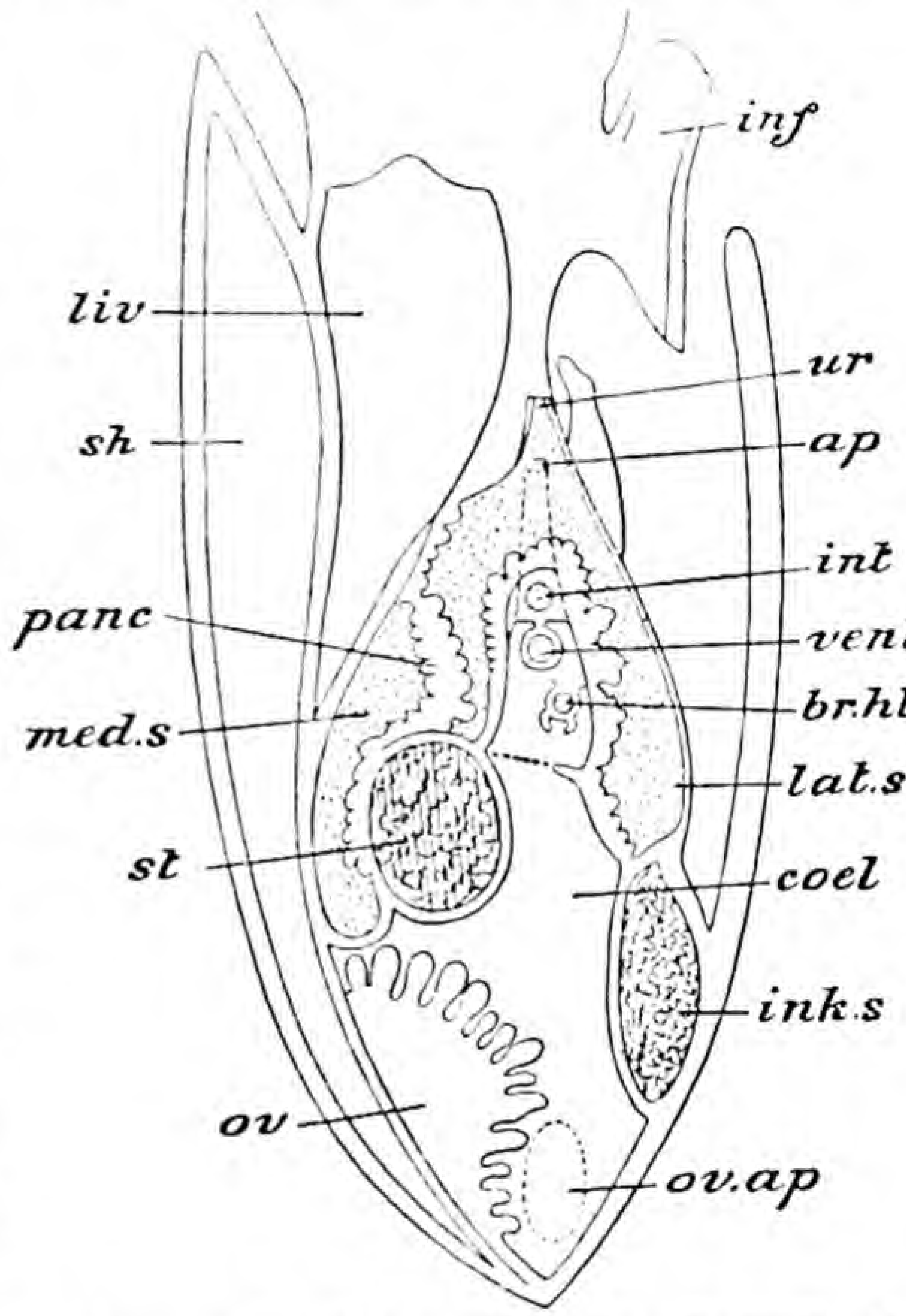


FIG. 628.—**Sepia officinalis,** diagram of a median vertical section of a female specimen, to show the relations of the cavities. *ap.* aperture between the pericardial part of cœlome and the lateral renal sac; *br. ht.* branchial heart; *cœl.* cœlome; *inf.* funnel; *ink. s.* ink-sac; *int.* intestine; *lat. s.* lateral renal sac; *liv.* liver; *med. s.* median renal sac; *ov.* ovary; *ov. ap.* aperture leading from oviduct to secondary body-cavity; *panc.* pancreatic appendages; *sh.* shell; *st.* stomach; *ur.* ureter; *vent.* ventricle. (From Vogt and Jung, after Grobben.)

Reproductive system.—In the male the *testis* (Fig. 629, *te.*) forms a compact mass of minute tubules situated in the aboral region of the body and enclosed in a capsule. The single spermiduct (*v. def.*) is a greatly convoluted tube which leads from the cavity of the capsule towards the left; it opens into an elongated *vesicula seminalis* (*ves.*), to which is appended a glandular body, the *prostate* (*pr.*). In the interior of the vesicula seminalis the sperms are rolled up by the action of a system of grooves and ridges into long narrow bundles of about 2 cm. in length, each of which becomes enclosed by a chitinoid capsule of a narrow cylindrical shape, forming a *spermatophore* (Fig. 630, *B*); at one end of the spermatophore is a complicated apparatus of the nature of a spring for causing the rupture of the wall and the discharge of the sperms. The vesicula seminalis expands into a wide sac—the *spermatophoral sac* or *Needham's sac* (Fig. 629, *sp. s.*)—in the interior of which the spermatophores are stored. This opens into the mantle-cavity by the aperture already described at the extremity of the penis to the left of the middle line.

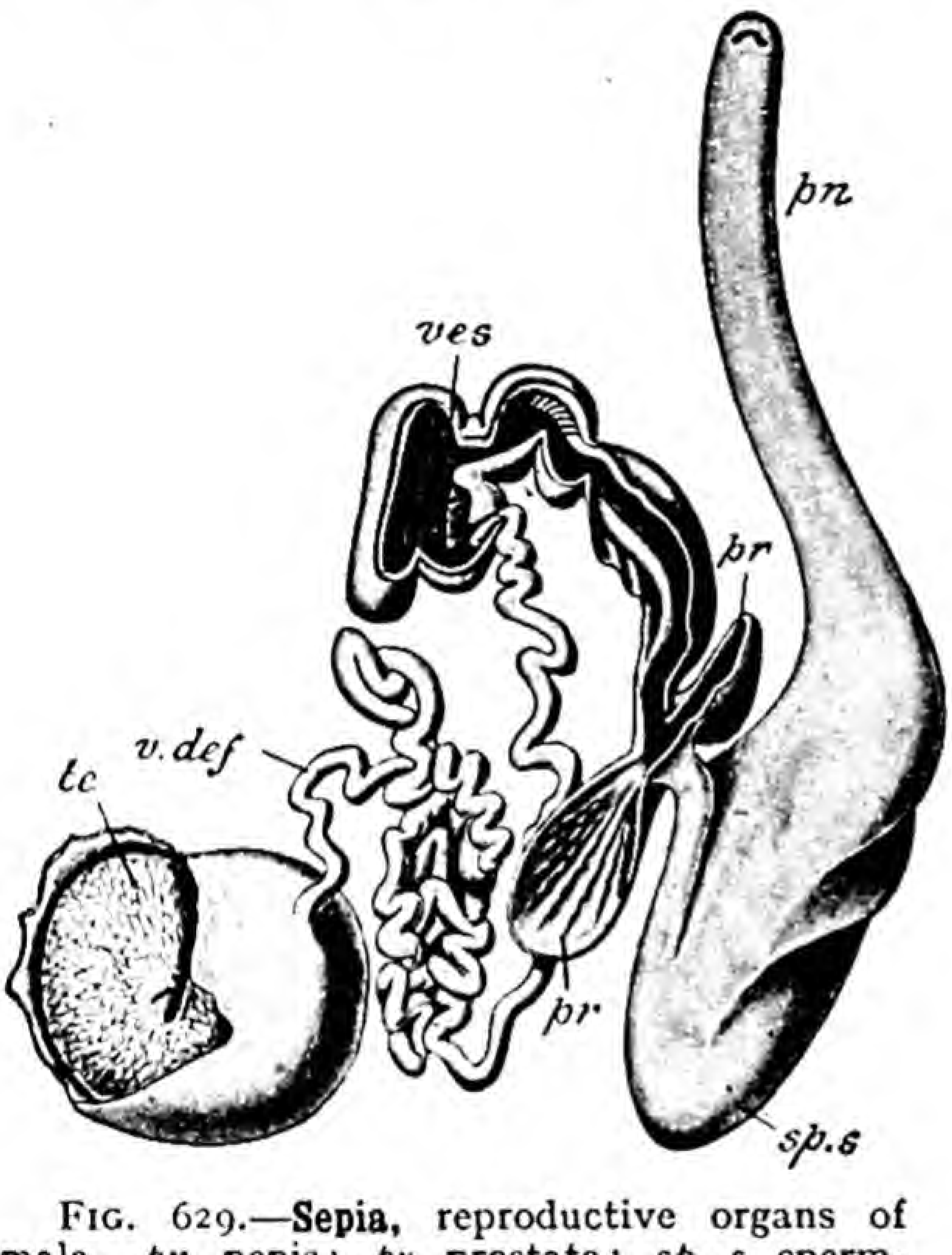


FIG. 629.—**Sepia,** reproductive organs of male. *pn.* penis; *pr.* prostate; *sp. s.* sperm-sac; *te.* testis; *v. def.* vas deferens; *ves.* vesicula seminalis. (After Keferstein.)

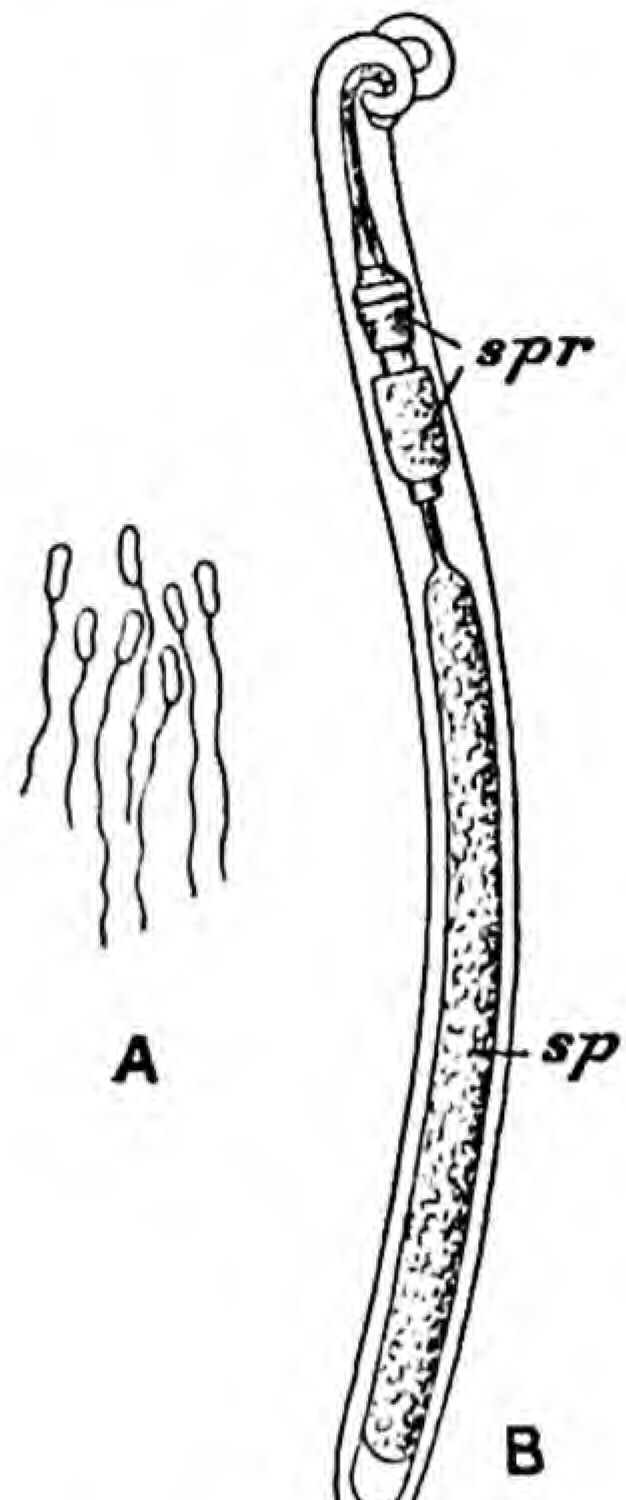


FIG. 630.—**Sepia.** *A*, sperms, highly magnified; *B*, spermatophore. *sp.* mass of sperms; *spr.* spring apparatus by which the wall of the spermatophore is ruptured. (From Vogt and Jung.)

In the female the *ovary* (Fig. 614, *ov.*) occupies a position corresponding to that of the testis in the male, and is enclosed in a similar capsule, with the cavity of which the lumen of the oviduct is continuous. An axial swelling bears

numerous follicles, each containing a single ovum supported on a long slender stalk; the different ova are in various stages of development. At the breeding season the ovary becomes a compact mass of ova, which assumes a polygonal shape owing to mutual pressure. The *oviduct* (*ovid.*) is a wide tube, opening as already described, into the mantle-cavity to the left of the rectum. Occupying a conspicuous position on the anterior wall of the mantle-cavity of the female is a pair of large flattened glands of somewhat oval outline, the *nidamental glands* (*nid.*), situated to the right and left of the ink-duct. In the long axis of each is a median canal, on either side of which is a range of closely-set delicate lamellæ; the median canal opens into the mantle-cavity by a slit bounded by a number of plaits situated at the narrower oral end. The nidamental glands secrete the viscid material by means of which the eggs when deposited adhere together in masses. A glandular mass of unknown function, known as the *accessory nidamental glands* (*ac. nid.*), lies at the sides and around the oral ends of the nidamental glands proper.

(*b*) The Pearly Nautilus (*Nautilus pompilius*).

The three living species of Nautilus, of which *N. pompilius* is the best known, are inhabitants of moderately shallow water about the shores and coral-reefs

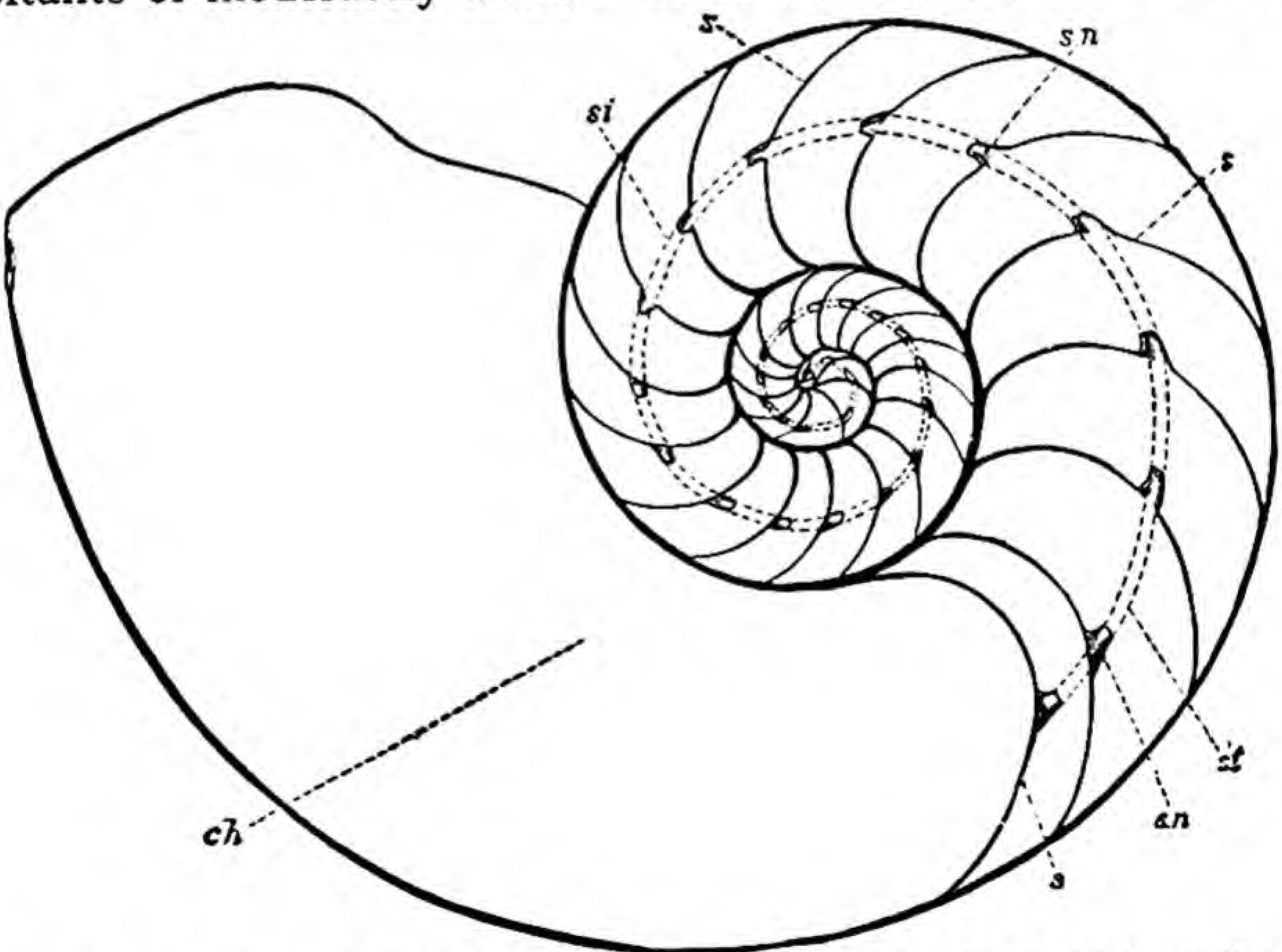


Fig. 631.—Section of the shell of **Nautilus pompilius,** showing the septa (*s, s*), the septal necks (*s. n., s. n.*), the siphuncle, *si.* (represented by dotted lines), and the large body-chamber (*ch.*). (From the *Cambridge Natural History.*)

of the South Pacific, usually swimming near the bottom, and probably rarely, if ever, coming voluntarily to the surface. The body is enclosed in a calcareous, spirally-coiled **shell** (Fig. 631), into which the entire animal can be withdrawn

for protection. The cavity of the shell is divided by a system of *septa* into a series of chambers, the last and largest of which, opening widely on the exterior, alone lodges the body of the animal. Between the animal and its shell there is a direct organic connection through the intermediation of a narrow,

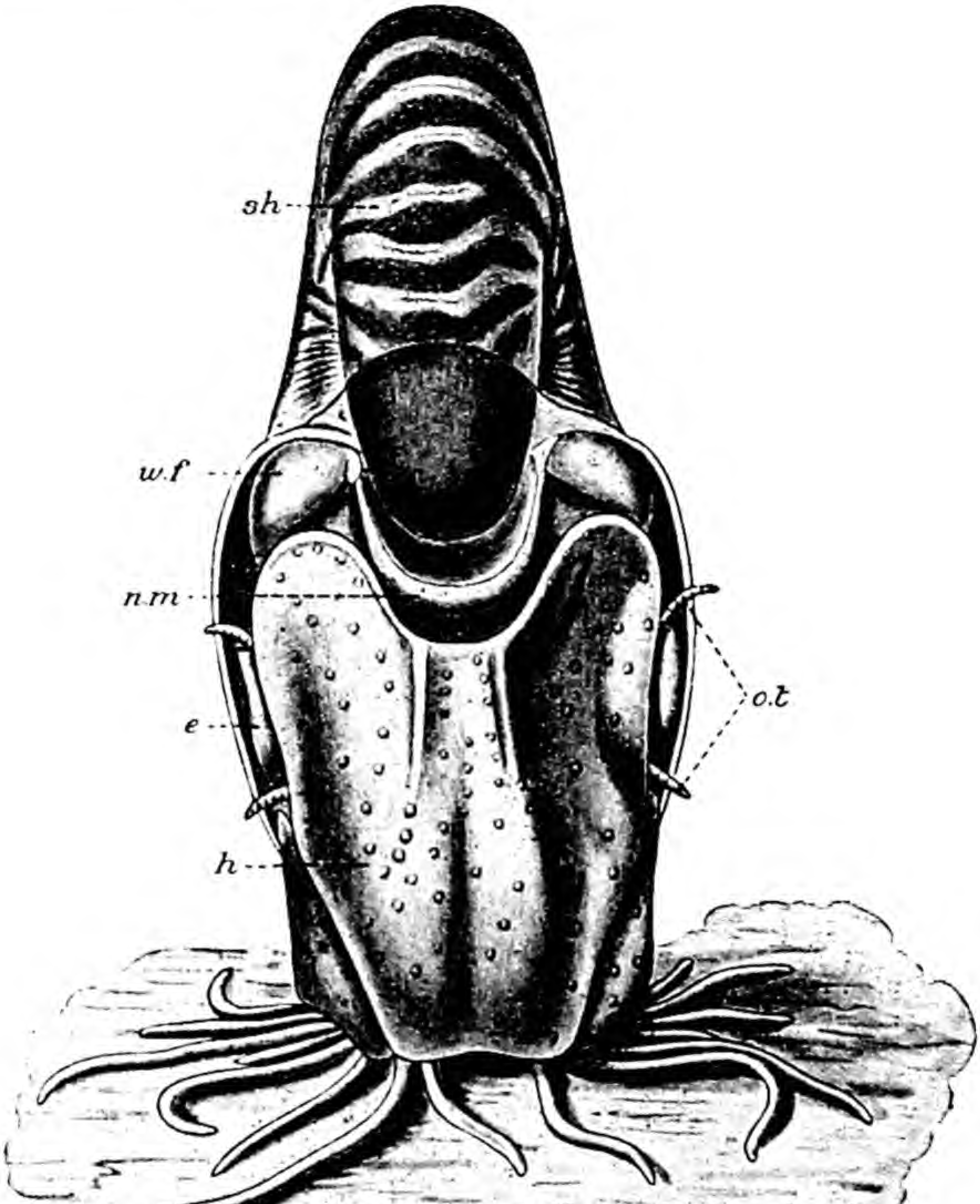


FIG. 632.—**Nautilus macromphalus**, adhering to the substratum in a vertical position by means of its tentacles. *e.* eye; *h.* hood; *n. m.* nuchal membrane detached from coil of shell; *o. t.* ophthalmic tentacles; *sh.* shell; *w. f.* wing of funnel. (After Willey.)

tubular, vascular prolongation of the visceral region, which perforates the entire series of the septa to the apex of the spiral. This tube, which is termed the *siphuncle* (*si.*), has its wall supported by scattered spicules of carbonate of lime; but, in addition, as it passes through each septum, there is produced over it for some distance a shelly tube—the *septal neck* (*s. n.*)—continuous with the

substance of the septum. The apical or initial chamber presents a small scar, the *cicatrix*, which may indicate the original presence of the larval shell, or *protoconch*, which has fallen off in the course of development.

When the animal is removed from the shell it is found to possess two regions, a distinct and relatively large, obtusely conical *head* (cephalopodium) bearing eyes and a system of tentacles, and a rounded sac-like *trunk*. The mouth, situated at the free extremity, is provided with a pair of relatively enormous, partly calcified jaws. Surrounding the mouth is a series of bilaterally arranged lobes which represent the forefoot or the epipodia of other Molluscs. These are beset with numerous slender, three-sided tentacles, each provided with an elongated tubular sheath, in the interior of which the greater part of the tentacle in the retracted condition lies enclosed, only a small portion protruding. Minute ring-like markings on the tentacles are due to the presence of a number of annular constrictions, which give the tentacles a transversely ridged character. There are no suckers: but the ridged surfaces enable the tentacles to adhere firmly to rough objects. The tentacles are arranged in two series, an outer and an inner. The outer, which are borne on an annular muscular ridge of the foot, are nineteen on each side in both sexes. Anteriorly this muscular ridge is thickened to form a massive lobe—the *hood* (Fig. 632, *h.*)—in which there is a concavity for the reception of the coil of the shell. The hood bears two tentacles, and has the appearance of being composed of the immensely developed sheaths of these, completely fused together in the middle line: on each side the enlarged sheaths of a second pair of tentacles are closely applied to, though not completely coalescent with, the hood, being separated from the latter by a narrow groove. The hood with these two enlarged sheaths, is covered with a thickened tuberculated skin, and acts after the manner of an operculum for protecting the tentacles and other soft parts about the head. Altogether there are forty-two tentacles of the outer series, including four *ophthalmic* tentacles (Fig. 633, *i.*, *k.*), one situated on the oral and another on the aboral side of each eye. The latter (ophthalmic) differ from the rest in being highly sensitive, ciliated, and with the ridges on the inner side produced into lamellæ. The tentacles of the inner series differ strikingly in number and arrangement in the two sexes. In the female there are two inner lateral lobes, right and left, quite symmetrically developed, each bearing twelve tentacles, and an inner posterior lobe (Fig. 633, c.) divided by a deep median notch into two, each half bearing twelve to fourteen tentacles. On the middle of the oral surface of the latter, close to the median notch, is an oval patch raised up into numerous closely set ridges (*organ of Owen*, Fig. 633, *n.*).

In the male the inner posterior lobe with its ridged organ is only represented by a median posterior body consisting of two oval elevations, each divided into a number of folds (*organ of van der Hoeven*, Fig. 633, *d.*). The internal lateral lobes are greatly modified, four of the tentacles on either the right side or the

left, usually the latter, being modified to form a structure termed the ***spadix*** (Figs. 633, *p.*, 634), which is supposed to represent the hectocotylized arm of the male *Sepia*. It has the form of a large compressed cone formed by the union of the enlarged sheaths of three of the tentacles. The corresponding

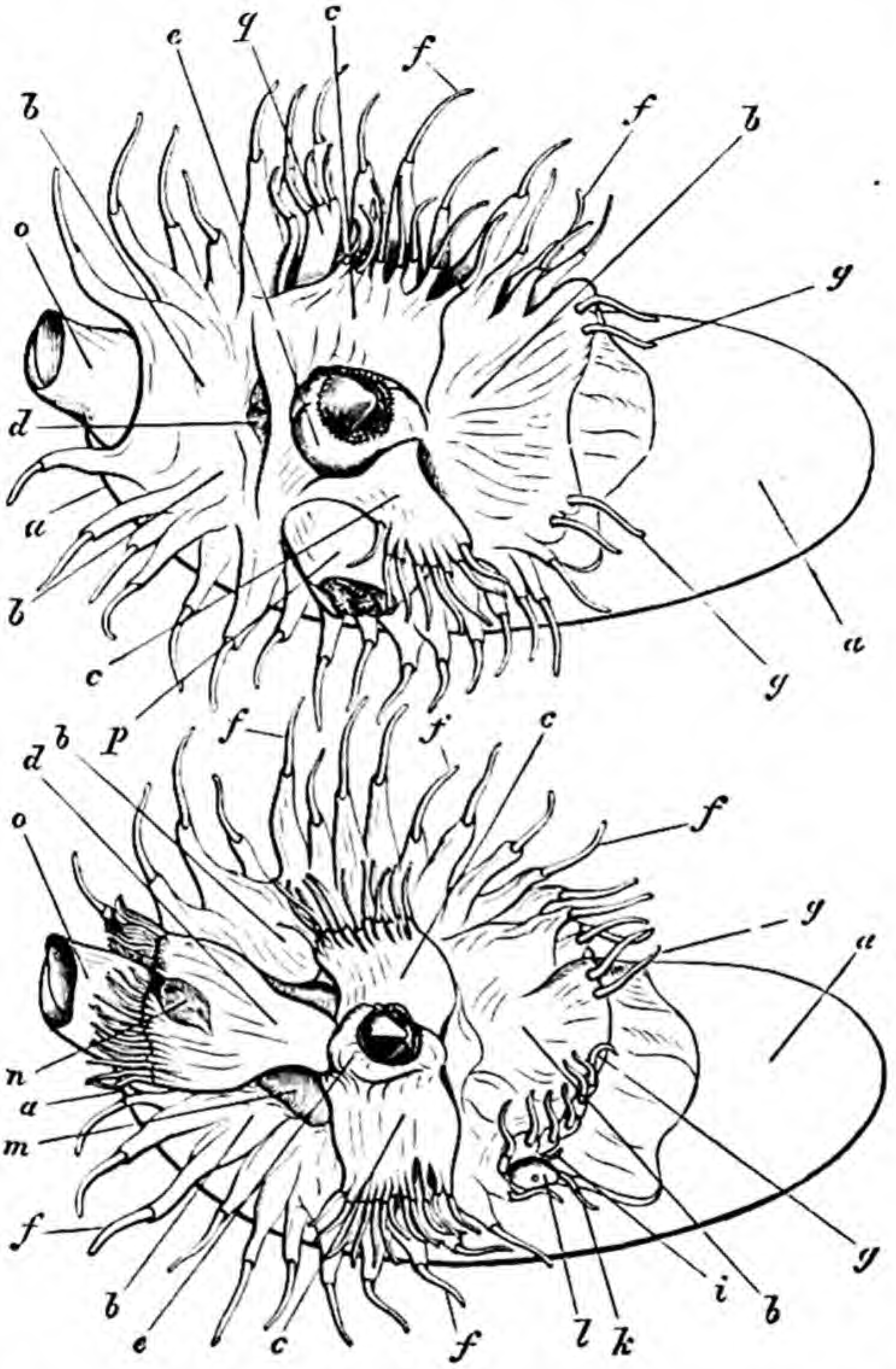


FIG. 633.—Male (upper) and female (lower) specimens of **Nautilus pompilius**; oral view showing the disposition of the tentaculiferous lobes in the two sexes. *a.* shell; *b.* outer annular lobe of foot; *c.* right and left inner lobes of foot; *d.* inner inferior lobe of foot (organ of van der Hoeven in male); *e.* buccal cone; *f.* tentacles of outer lobe; *g.* the two most posterior tentacles; *i.* superior ophthalmic tentacle; *k.* inferior ophthalmic tentacle; *l.* eye; *m.* paired lamellated organ (organ of Valenciennes); *n.* lamellated organ of Owen; *o.* funnel; *p.* spadix; *q.* anti-spadix. (From Lankester's *A Treatise on Zoology* (Adam & Charles Black).)

tentacles themselves are in the adult male enormously thickened, and the outer surface of the most posterior (3) is covered with regularly arranged rows of minute pits. A fourth tentacle, much smaller than the others, is closely applied to the outer surface of the organ. In the internal lateral lobe, right or left as

the case may be, opposite that bearing the spadix, the latter is represented by a group of four tentacles forming what is termed the *anti-spadix* (Fig. 633, *q.*)

A further difference between the male and the female with regard to the foot is the presence in the latter, but not in the former, on the inner surface of the outer ring, close to the inner posterior lobe on either side, of an area thickly beset with delicate membranous ridges (*organ of Valenciennes*, Fig. 633, *m.*).

On the posterior side of the head is a funnel (*o.*) corresponding with that of Sepia, but extending farther forwards; this, however, does not form a completely closed tube, the edges of its right and left halves being simply in apposition posteriorly without being united together. Near the oral end is a large, somewhat triangular valve arranged like that of Sepia.

There is an internal skeleton of cartilage (Fig. 635), as in Sepia, but its relationships with the nerve ganglia are much less intimate in the case of Nautilus than in that of Sepia.

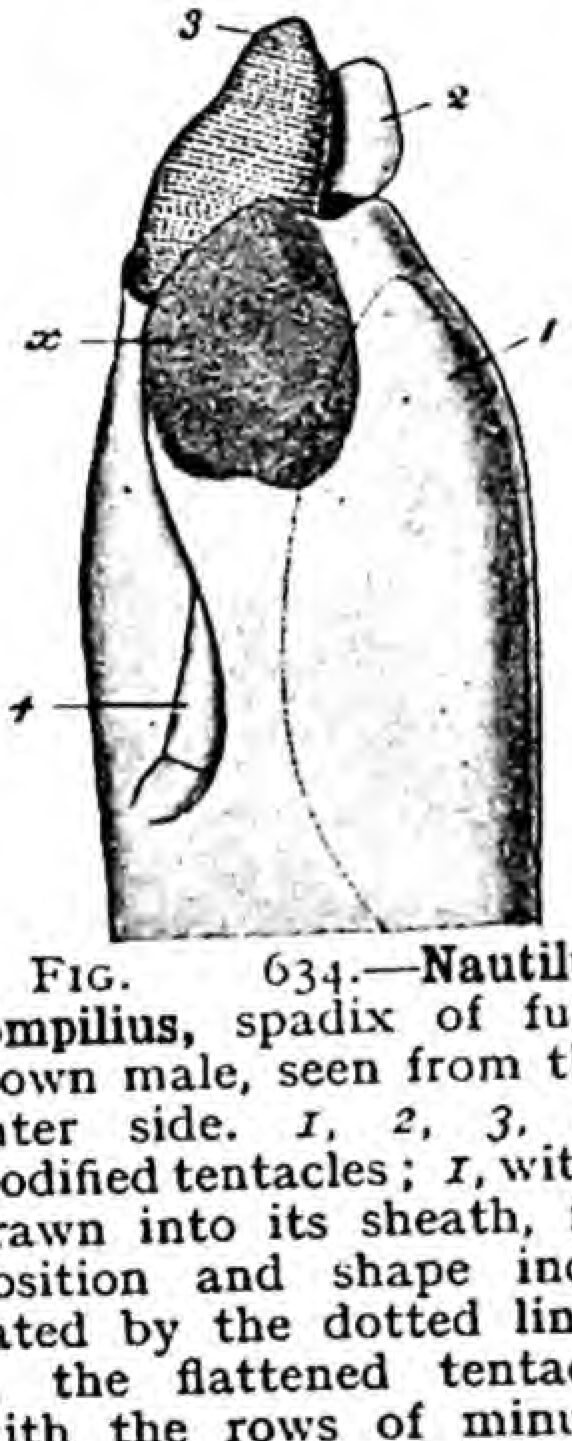


FIG. 634.—**Nautilus pompilius,** spadix of full-grown male, seen from the outer side. *1*, *2*, *3*, *4*, modified tentacles; *1*, withdrawn into its sheath, its position and shape indicated by the dotted line; *3*, the flattened tentacle with the rows of minute cavities; *x*, patch of modified integument. Two-thirds of the natural size. (After Haswell.)

FIG. 635.—**Nautilus pompilius,** cartilaginous internal skeleton. (After Keferstein.)

Mantle and Mantle-cavity.—The mantle is produced around the head into a free flap, longer and looser than the mantle-flap of Sepia. Dorsally this splits into two layers, reflected over the convexity of the shell, which fits into a hollow behind the hood. Ventrally and posteriorly the mantle encloses a large mantle-cavity (Fig. 636), corresponding to that of Sepia. In this are lodged two pairs of ctenidia (*cten.*), having the same general structure as the single pair present in Sepia. Between the bases of the ctenidia of each side is a small knob-like elevation, the *oral osphradium* (*ant. os.*),[1] and behind the bases of the more

[1] As in Sepia, it is convenient to use the term *oral* for parts towards the mouth end, and *aboral* for those situated towards the opposite extremity, the same terms being also used to indicate *relative* position of different parts. The relative position of the parts is, however, for the sake of simplicity given here as they lie when the mantle-cavity is opened by turning back its thin postero-ventral wall.

aborally situated pair are two compressed, bilobed projections, more or less completely united in the middle so as to form a transverse ridge; these are the *aboral osphradia* (*p. os.*). In the middle line of the mantle-cavity is the *anus* (*an.*), a large aperture with minutely lobed margin, situated on a slight elevation, but by no means so prominent as in Sepia. On each side are two apertures, the

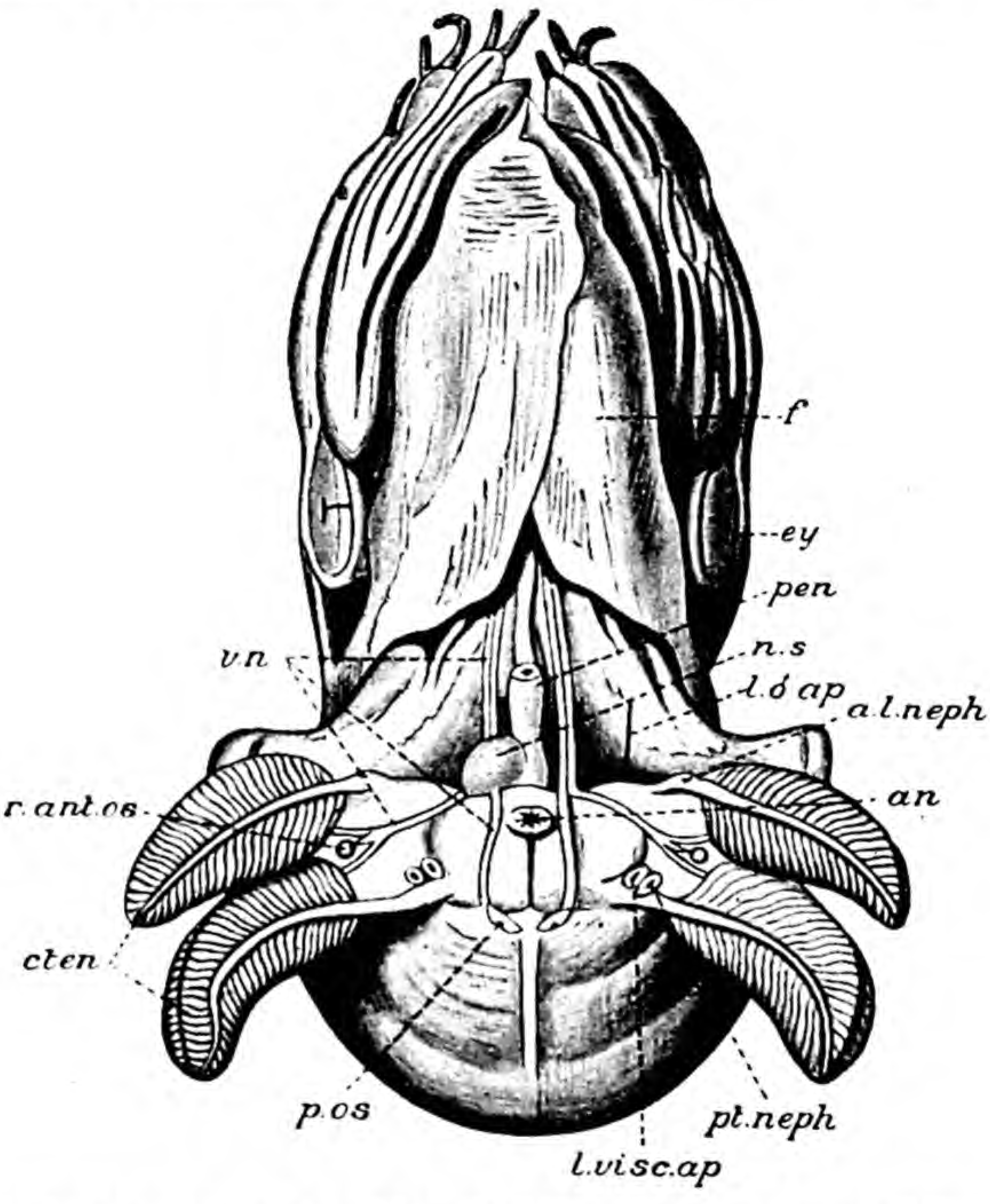


FIG. 636.—**Nautilus pompilius,** interior of mantle-cavity of a male specimen with the postero-ventral wall reflected. *a. l. neph.* oral left renal aperture; *an.* anus; *cten.* ctenidia; *ey.* eye; *f.* funnel; *l. ♂ ap.* left reproductive aperture indicated by a bristle passed through it; *l. visc. ap.* left viscero-pericardial aperture; *n. s.* Needham's sac; *pen.* penis; *pt. neph.* aboral left renal aperture; *p. os.* aboral osphradia; *r. ant. os.* right oral osphradium; *v. n.* visceral nerves. (After Willey.)

oral and aboral *renal apertures* (Fig. 636, *a. l. neph.*, *pt. neph.*), corresponding to the single pair of Sepia, but not elevated on papillæ. Close to each posterior renal aperture is an opening—the *viscero-pericardial aperture* (*l. visc. ap.*, *r. visc. ap.*)—leading into the pericardial section of the cœlome; these are not represented in Sepia. In both sexes there are two reproductive ducts, right and left; but in both the right alone appears to be functional, and the left is

much the smaller. The opening of the right sperm-duct of the male is situated on a cylindrical prominence—the *penis* (*pen.*)—placed close to the middle line. In the female the nidamental glands are, as in Sepia, conspicuous objects when the mantle-cavity is exposed; but they are mainly situated on its posterior instead of its anterior wall.

Enteric Canal.—The mouth is surrounded by a circular lip beset with numerous papillæ. There is a pair of jaws (Fig. 637, *jaw*) of similar shape to those of Sepia, but much more powerful, and calcified towards the tips. The buccal mass is a large rounded body with thick muscular walls. On the floor of the buccal cavity is a large and prominent odontophore (*odont.*), with long and pointed, curved teeth. In front of the odontophore is a large bilobed soft prominence, the *tongue* (*tong.*). Behind the odontophore, between it and the opening of the œsophagus, are one large median and two lateral tongue-like prominences beset with papillæ; on the inner surface of the latter are the apertures of a pair of salivary glands.

The œsophagus (*œs.*) becomes dilated aborally into a very spacious *crop* (*cr.*) for the storage of the food, which consists of small prawn-like Crustaceans and small Fishes broken up by the jaws and radula. This opens into a rounded stomach (*stom.*) having very much the appearance of the gizzard-like cæcum of Sepia. The intestine (*int.*) shortly after it leaves the stomach, develops a rounded cæcum (*cæc.*) with complexly folded walls, into which the ducts of the digestive gland or "liver" open. The intestine does not pass straight to the anus as in Sepia, but first bends round in a short coil. The ink-sac and duct of Sepia are not represented. There is a very large digestive gland divided into four main portions or lobes, each of which is made up of a number of lobules. The ducts ("bile-ducts," *b. du.*), opening as above mentioned into the cæcum, have a series of small diverticula, which may represent the pancreatic appendages of Sepia.

The **cœlome** consists of the *pericardium* and the *gonocœle*—the cavity in which the gonad is enclosed: these communicate with one another by three apertures. The pericardium contains the ventricle, the four auricles, and the parts of the renal glandular appendages. It communicates with the exterior by the viscero-pericardial apertures.

Heart and Vascular System.—The blood-system consists of the heart, the arteries and veins, and certain large spaces constituting the hæmocœle. The latter consists of three chief parts—the peristomial, peri-œsophageal, and peri-hepatic hæmocœles, the first surrounding the buccal mass, the second the œsophagus, and the third the liver.

The ventricle (Figs. 637 and 639, *vent.*) is a bilobed, transversely placed, muscular sac, very similar to that of Sepia. On either side there open into it two *auricles* or *efferent branchial vessels*, one from each of the four ctenidia. The ventricle gives off a large main *aorta* (*aort.*), which passes to the head after giving off

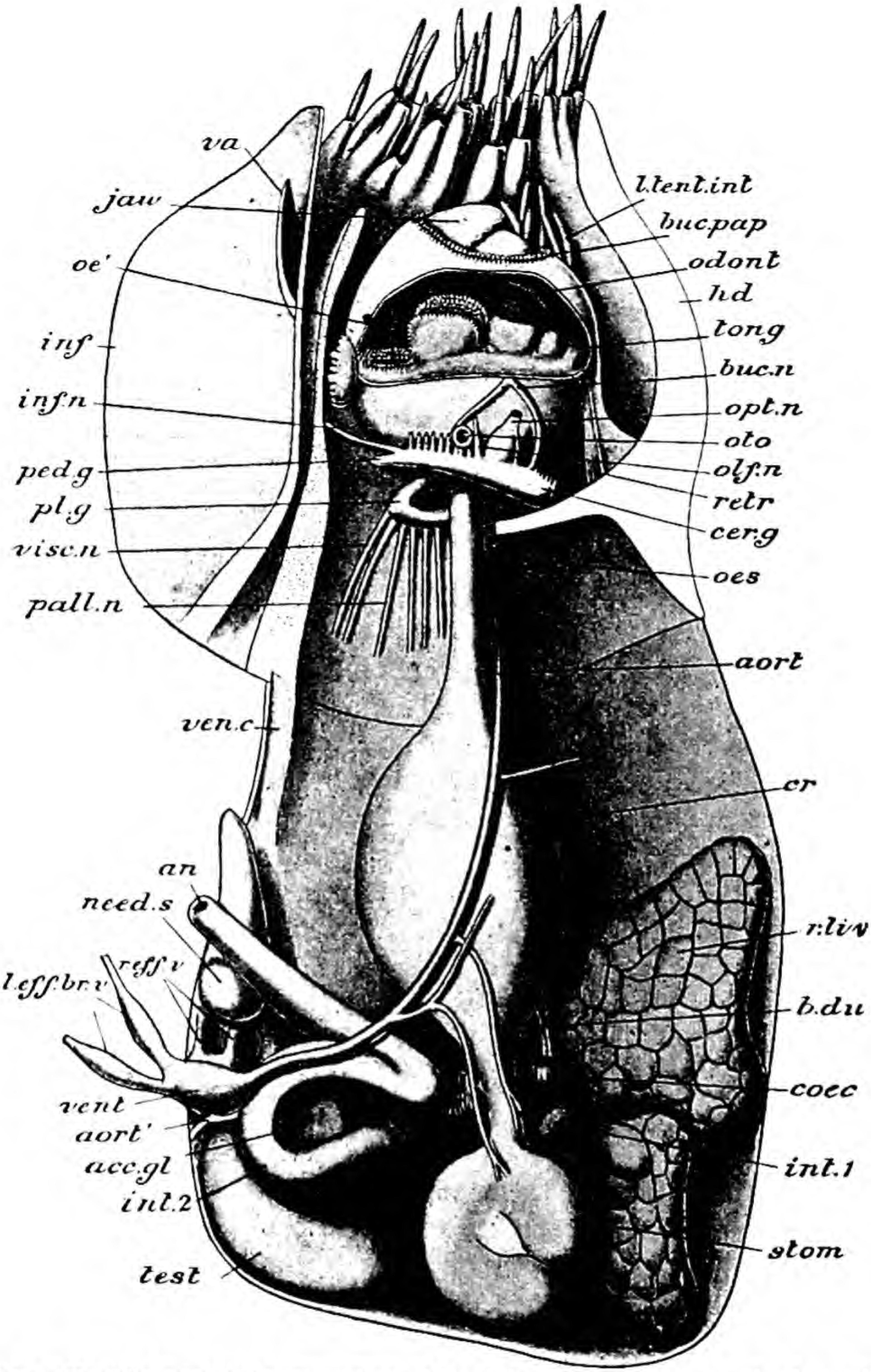


FIG. 637.—**Nautilus pompilius,** dissection of the internal organs of a male, from the left side. The funnel and the hood have been divided by a longitudinal median section. A portion of the wall of the buccal cavity has been removed to show the odontophore and the tongue. *acc. gl.* vesicula seminalis; *an.* anus; *aort.* oral aorta; *aort'.* posterior pallial artery; *b. du.* bile-ducts; *buc. n.* buccal nerves; *buc. pap.* papillæ of peristomial membrane; *cer. g.* cerebral ganglion; *cœc.* cæcum; *cr.* crop; *hd.* hood; *inf.* funnel; *inf. n.* infundibular nerve; *int. 1,* part of intestine between stomach and cæcum; *int. 2,* part of intestine following cæcum; *jaw,* larger (posterior) jaw; *l. eff. br. v.* left efferent branchial vessels; *l. tent. int.* left internal tentacular lobe; *need. s.* Needham's sac; *odont.* odontophore; *œ'.* style passed from buccal cavity into the opening of the œsophagus; *œs.* œsophagus; *olf. n.* olfactory nerve; *opt. n.* optic nerve; *oto.* statocyst; *pall. n.* pallial nerves; *ped. g.* pedal ganglion; *pl. g.* pleural ganglion; *r. eff. v.* right efferent branchial vessel; *retr.* retractor muscle of the buccal mass; *r. liv.* right lobe of "liver"; *stom.* stomach; *test.* testis; *tong.* tongue-shaped elevation of the floor of the mouth; *va.* valve of funnel; *ven. c.* vena cava; *vent.* ventricle.

arteries to the stomach, the crop, the digestive gland, and the mantle. From the aboral surface of the ventricle arises a smaller artery, the *lesser aorta*, which immediately bifurcates. One of its branches—the *posterior pallial artery* (Fig. 638, *post. pall. a.*)—passes to the area of the mantle applied to the septum, bifurcates to supply this area, and gives off a branch to the siphuncle. The other—*anterior pallial* (*ant. pall. a.*)—after giving off arteries to the intestine and rectum, and to the branchiæ and osphradia, passes to the muscular edge of the mantle, bifurcating anteriorly. Three *genital* arteries (*gen. a. 1, 2, 3*), supplying the various parts of the reproductive apparatus, are likewise given off directly from the ventricle.

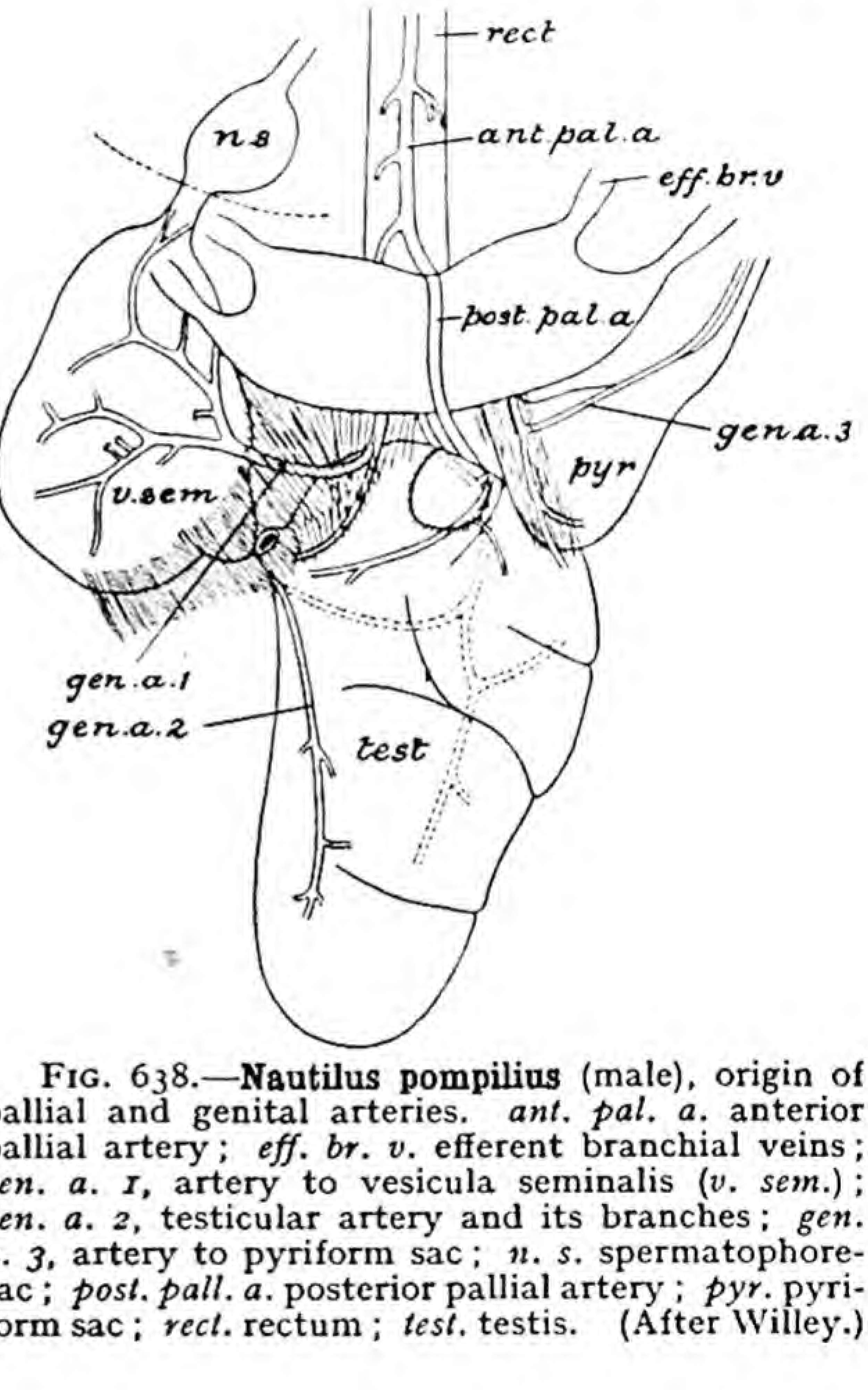


FIG. 638.—**Nautilus pompilius** (male), origin of pallial and genital arteries. *ant. pal. a.* anterior pallial artery; *eff. br. v.* efferent branchial veins; *gen. a. 1,* artery to vesicula seminalis (*v. sem.*); *gen. a. 2,* testicular artery and its branches; *gen. a. 3,* artery to pyriform sac; *n. s.* spermatophore-sac; *post. pall. a.* posterior pallial artery; *pyr.* pyriform sac; *rect.* rectum; *test.* testis. (After Willey.)

A large *vena cava* (Figs. 637 and 639, *ven. c.*) occupies a position corresponding closely with that which it occupies in Sepia. It presents the remarkable peculiarity of being in free communication by numerous (valvular) apertures with the general cavity of the hæmocœle. At its aboral end it presents a dilatation from which four *afferent branchial veins* (Fig. 639, *a. l. aff, p. l. aff, p. r. aff., r. ant. aff.*)—two right and two left—proceed to the corresponding ctenidia, at the bases of which veins from the aboral region join them. There are no branchial hearts.

The **renal organs** (Fig. 639) are, like the ctenida and the afferent and efferent vessels, four in number instead of two as in Sepia. Each renal sac (*l. neph. s., r. neph. s., l. post. neph. s., r. post. neph. s.*) opens into the mantle-cavity, as already stated, by an orifice which is not drawn out into a tube. There is no communication between the cavities of the different sacs, and thus no median chamber as in Sepia, and there is also no communication with the pericardium. The cavities are found to contain phosphate of lime. Into each projects, from the corresponding afferent branchial vein, a compact rounded group of venous appendages (*ren. app.*), consisting of two symmetrical portions. Internal to these, each afferent vein has connected with it a second group of glandular

appendages, which are cylindrical or club-like in form ; they project, not into the renal sac, but into the pericardial compartment of the cœlome. They have been compared with the appendages of the branchial heart of Sepia, but differ in their relations to the renal appendages.

Nervous System.—Nautilus differs strikingly from Sepia, in the form assumed by the central parts of the nervous system (Fig. 637, *cer. g.*), distinct ganglia being absent. A very thick nerve-collar, the posterior portion of which is double, surrounds the œsophagus. The anterior part of the collar (Fig. 637, *cer. g.*) represents the cerebral ganglia, the oral portion of the posterior part the pedal (*ped. g.*), the aboral portion the pleuro-visceral (*pl. g.*) ; while the lateral

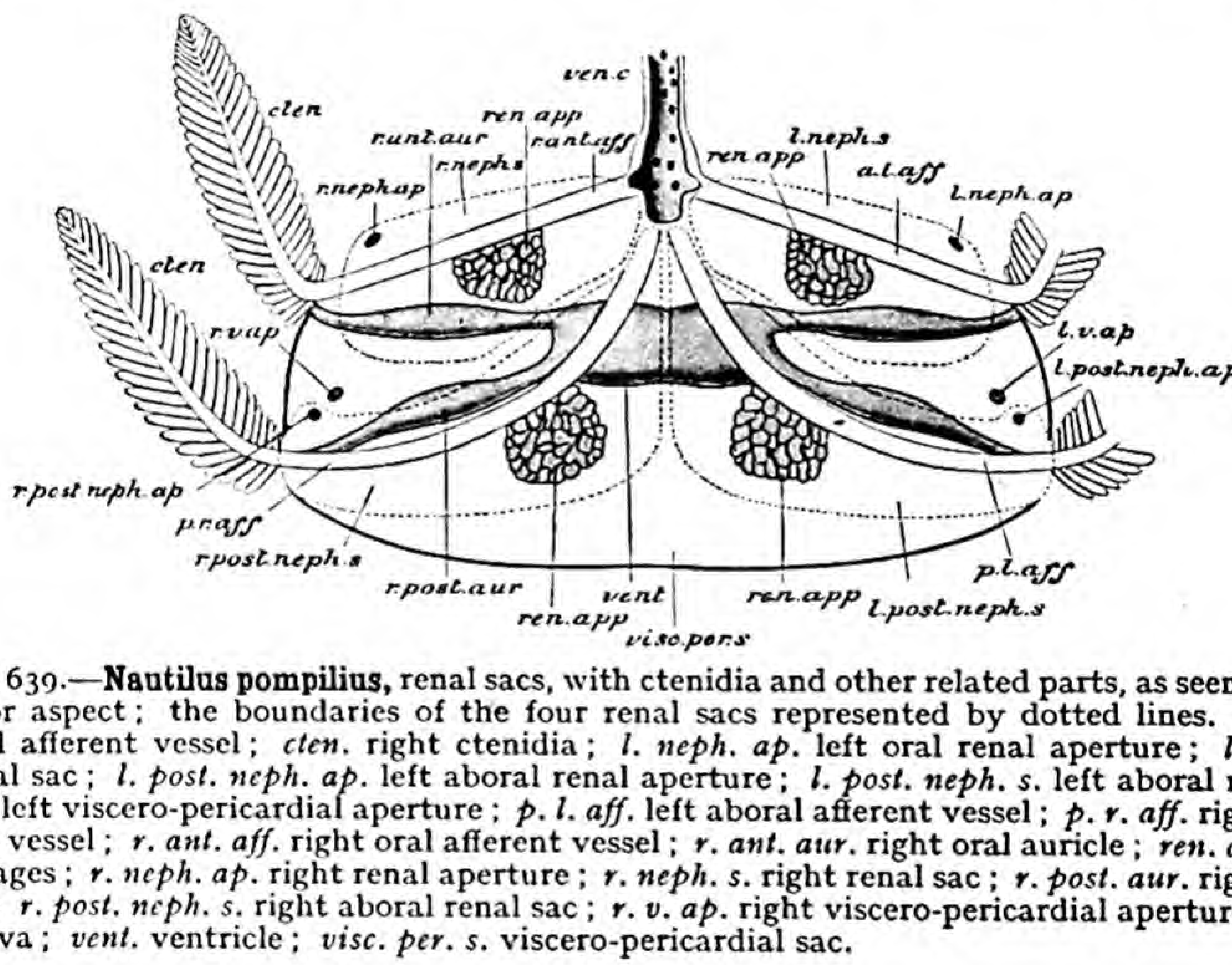


FIG. 639.—**Nautilus pompilius,** renal sacs, with ctenidia and other related parts, as seen from the posterior aspect ; the boundaries of the four renal sacs represented by dotted lines. *a. l. aff.* left oral afferent vessel ; *cten.* right ctenidia ; *l. neph. ap.* left oral renal aperture ; *l. neph. s.* left renal sac ; *l. post. neph. ap.* left aboral renal aperture ; *l. post. neph. s.* left aboral renal sac ; *l. v. ap,* left viscero-pericardial aperture ; *p. l. aff.* left aboral afferent vessel ; *p. r. aff.* right aboral afferent vessel ; *r. ant. aff.* right oral afferent vessel ; *r. ant. aur.* right oral auricle ; *ren. app.* renal appendages ; *r. neph. ap.* right renal aperture ; *r. neph. s.* right renal sac ; *r. post. aur.* right aboral auricle ; *r. post. neph. s.* right aboral renal sac ; *r. v. ap.* right viscero-pericardial aperture ; *ven. c.* vena cava ; *vent.* ventricle ; *visc. per. s.* viscero-pericardial sac.

parts, not distinctly marked off from the rest, represent the cerebro-pedal and cerebro-pleural connectives. From the cerebral ganglia pass nerves to the buccal mass, to the olfactory organs (*olf. n.*) and the statocysts, and a pair of very thick optic nerves supply the eyes (*opt. n.*). The pedal ganglion gives off numerous nerves to the tentacles and the funnel, and from the pleuro-visceral arise pallial and visceral nerves.

Sense-organs.—The *statocysts* are a pair of sacs embedded in recesses close to the cerebral ganglia, but not enclosed in the cartilage of the endoskeleton ; each contains a number of microscopic *statocones.* An olfactory function is ascribed to a process (the *rhinophore*) with a ciliated pit at its base, situated on the aboral side of the eye. The ophthalmic tentacles (Fig. 632, *o. t.*) are supposed

to act as accessory olfactory organs. The *osphradia* contain ganglion-cells and are beset with sensory cilia.

The *eyes*, situated at the sides of the head, are very large but extremely simple in structure, presenting a marked contrast to those of Sepia, and scarcely comparable to those of any other animal with the exception perhaps of Patella (p. 570). Each is of the shape of a saucer, attached to the head by its convex side by means of a short thick stalk, the mouth being closed in by a slightly convex disc; with a circular aperture at about its centre. A slightly raised rim runs round close to the margin on the posterior half, and a narrow groove extends inwards from this to the central aperture. In the interior of the cup is neither lens, vitreous humour, nor iris. The sea-water, passing in through the central aperture, directly bathes the retina, which is spread over the interior in a thick layer.

Reproductive Organs.—The gonad (testis, Fig. 640, *test.*, or ovary, Fig. 641,

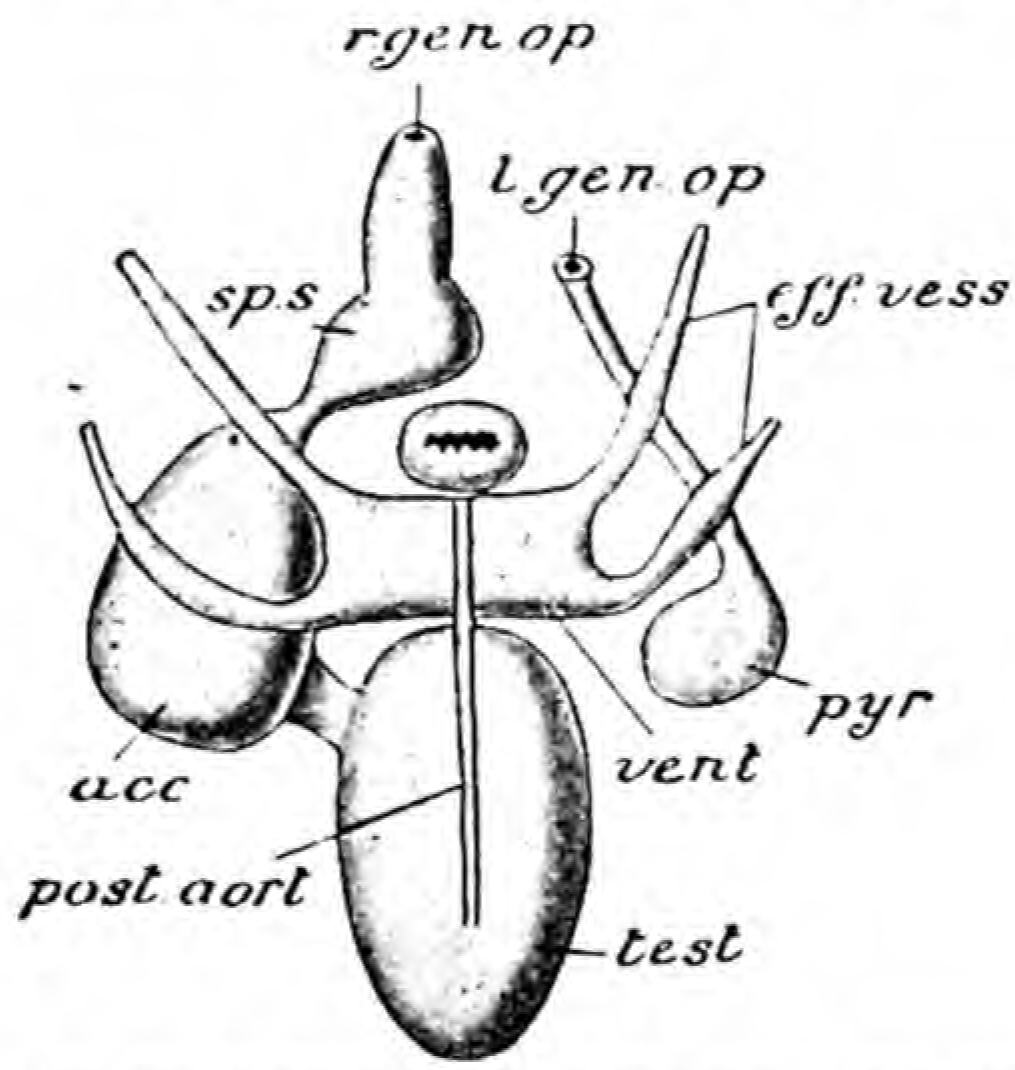


FIG. 640.—**Nautilus pompilius,** male reproductive organs. *acc.* vesicula seminalis; *eff. vess.* efferent branchial vessels; *l. gen. op.* left genital opening; *post. aort.* posterior aorta; *pyr.* pyriform appendage; *r. gen. op.* right genital opening; *sp. s.* spermatophore-sac; *test.* testis; *vent.* ventricle.

ov.), like that of Sepia, is single and median, enclosed in a special sac towards the aboral end of the body. The duct is paired in both sexes, but in both the right alone appears to be functional. In the male a large glandular *vesicula seminalis*, in which the spermatophores are formed (*acc.*), is connected with the right duct and this appears to be represented on the left-hand side by a vestige—the so-called *pyriform sac* (*pyr.*), situated close to the ventricle. The distal part of the right duct dilates to form a receptacle, the *spermatophoral sac* or *Needham's sac* (*sp. s.*), and opens, nearly in the middle line at the end of a prominence—the *penis* (Fig. 636, *pen.*). In the female the right oviduct has a glandular dilatation, which is supposed to be an albumen gland. The ova are of large size, greatly exceeding those of Sepia in dimensions, containing a large

proportion of food-yolk. Nidamental glands are present, but are mainly situated, as already pointed out, on the posterior instead of the anterior wall of

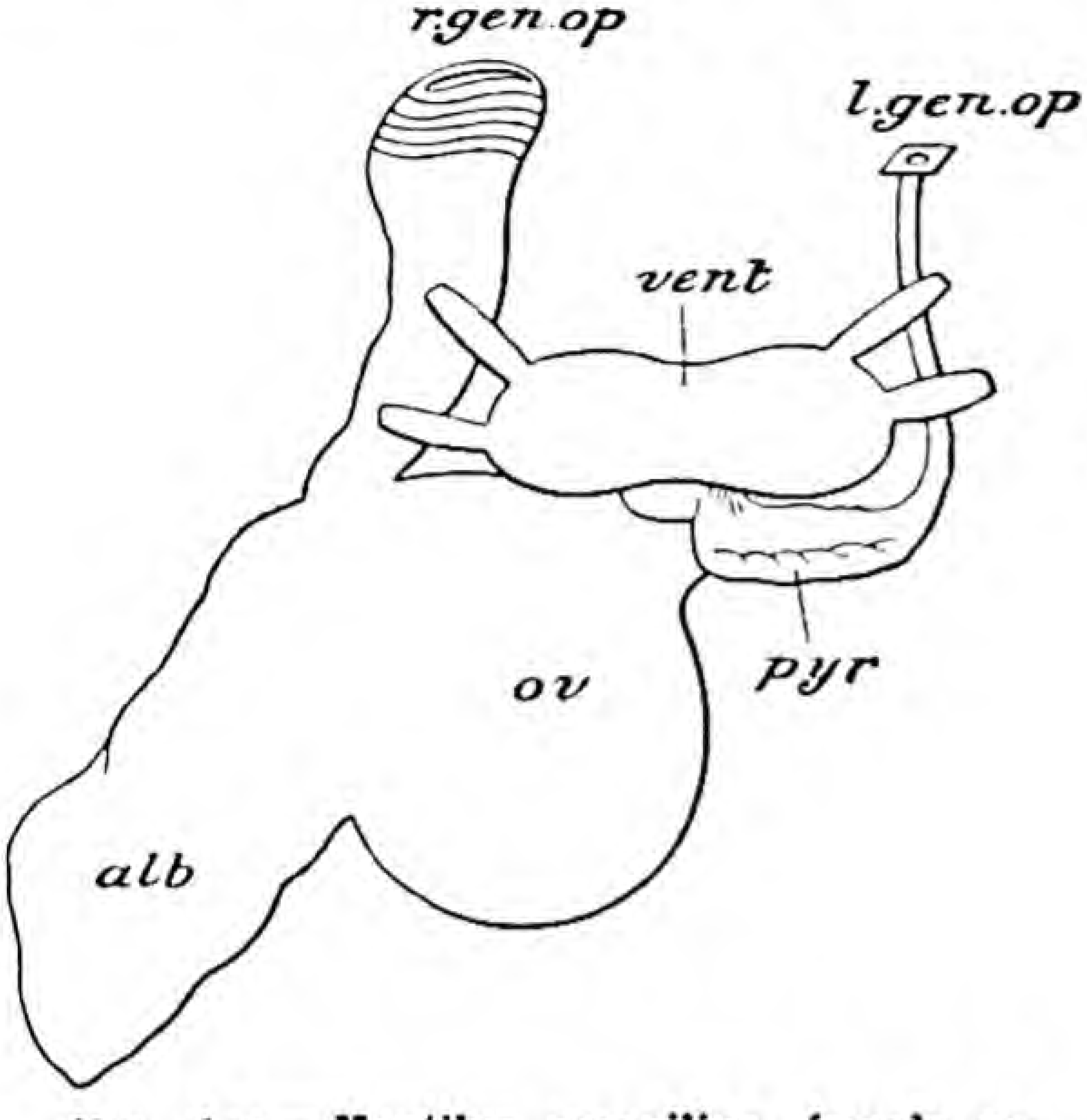


FIG. 641.—**Nautilus pompilius,** female reproductive organs. *alb.* albumen-gland; *l. gen. op.* left genital opening; *ov.* ovary; *pyr.* pyriform appendage; *r. gen. op.* right genital opening; *vent.* ventricle. (After Lankester and Bourne.)

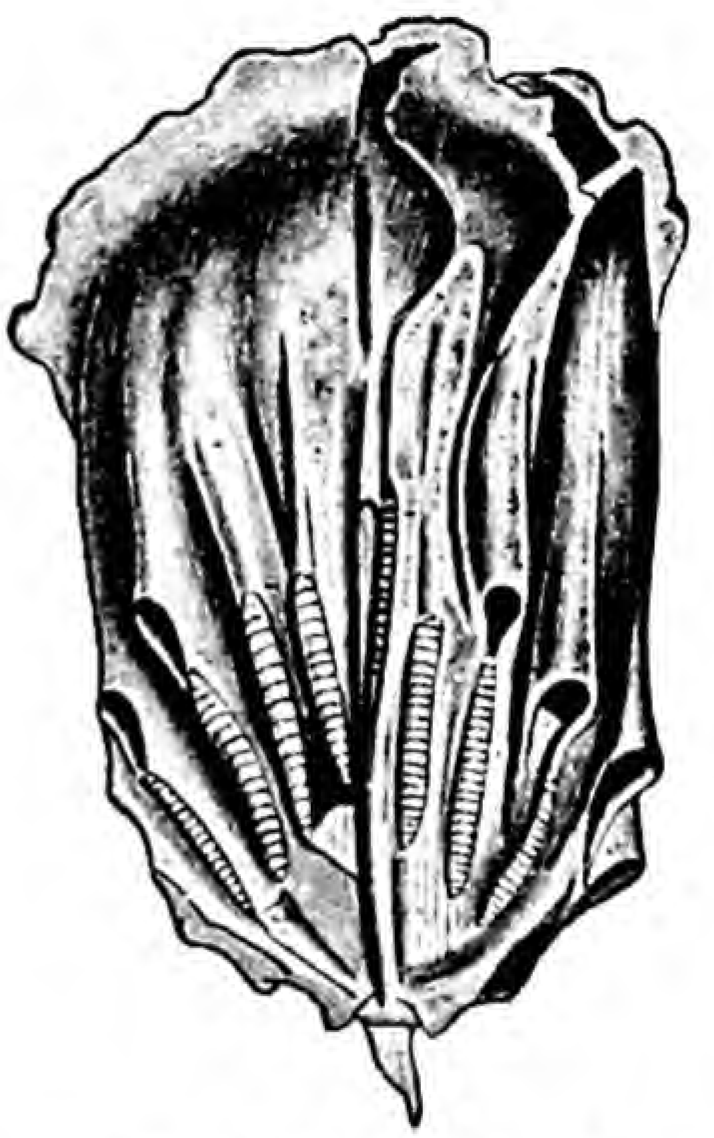


FIG. 642.—Egg of **Nautilus macromphalus,** enclosed in its capsule. (After Willey.)

the mantle-cavity. Each egg becomes enclosed in an elaborate capsule (Fig. 642), probably moulded by the agency of a nidamental gland. The development is not known.

2. Distinctive Characters and Classification.

The Cephalopoda are bilaterally symmetrical Mollusca, which have the main part of the foot displaced forwards to the neighbourhood of the mouth and divided into a series of arms bearing suckers or of lobes bearing tentacles, while the remainder of the foot forms a funnel for the egress of water from the mantle-cavity. The visceral mass is symmetrical and not coiled. The mantle encloses posteriorly and ventrally a large mantle-cavity, in which are situated the ctenidia and the renal, reproductive, and anal apertures. The shell may be absent or rudimentary; when present and well developed, it may be internal or external, undivided, or divided internally by septa into a series of chambers. There is an internal cartilaginous skeleton, supporting and protecting the nerve-centres and giving attachment to muscles. The mouth is provided with a pair of horny jaws, and an odontophore with a radula is present. In the majority there is an ink-gland with a duct opening into the rectum. The ctenidia and kidneys are either two or four in number.

The nervous system is highly developed; and the principal nerve-ganglia are aggregated together around the œsophagus. The sexes are separate; the cleavage of the ovum is meroblastic, and there is no metamorphosis.

Sub-Class I.—Belemnoidea (Dibranchiata).

Cephalopoda in which the main part of the foot assumes the character of a circlet of either eight or ten arms, bearing suckers, and surrounding the mouth. The funnel forms a complete tube. The shell is usually internal; when external its cavity is not divided by septa. There are two ctenidia, two kidneys, and two auricles. An ink-gland and duct are present.

ORDER 1.—DECAPODA.

Belemnoidea possessing ten arms, with stalked suckers provided with horny rims, and with a well-developed internal shell.

This order includes the Cuttle-fishes (*Sepia*, Fig. 613), *Architheutis*, Squids (*Loligo*, Fig. 644), *Spirula* (Fig. 649), and others, as well as the extinct Belemnites.

ORDER 2.—OCTOPODA.

Belemnoidea provided with eight arms, the suckers on which are sessile and devoid of horny rims: with or without slight vestiges of an internal shell. An external shell, secreted by a specially-modified pair of arms, is present in the female Argonaut only.

This order includes the Octopods (*Octopus*, Fig. 643) and the Argonauts (*Argonauta*, Fig. 645).

Sub-Class II.—Nautiloidea (Tetrabranchiata).

Cephalopoda in which the main part of the foot has the character of lobes bearing numerous tentacles. The funnel does not form a complete tube. There is an external, spiral, chambered shell. There are four ctenidia, four kidneys, and four auricles. An ink-gland is absent. The protoconch is represented only by a scar. The septal edges are simple.

This sub-class includes only one living genus, *Nautilus* (Fig. 632).

Sub-Class III.—Ammonoidea.

Cephalopoda, possibly tetrabranchiate, with an exogastrically-coiled shell, a persistent, globular protoconch, and typically with frilled septal edges.

This sub-class includes the extinct Ammonites (Fig. 650) and Goniatites.

3. General Organization.

The uniformity of structure among the Recent Belemnoid Cephalopoda is very great, and, as already stated, Nautilus is the only living member of the Nautiloidea, so that comparatively little has to be said to supplement the descriptions of the two examples.

External Features.—The general external shape differs very little in the different members of the Recent Belemnoidea: the body in some is more elongated than in others; the degree of compression likewise varies. Fins may be absent, and the animal may progress entirely by creeping with the aid of the long arms, or by swimming by the movements of the arms, or under the

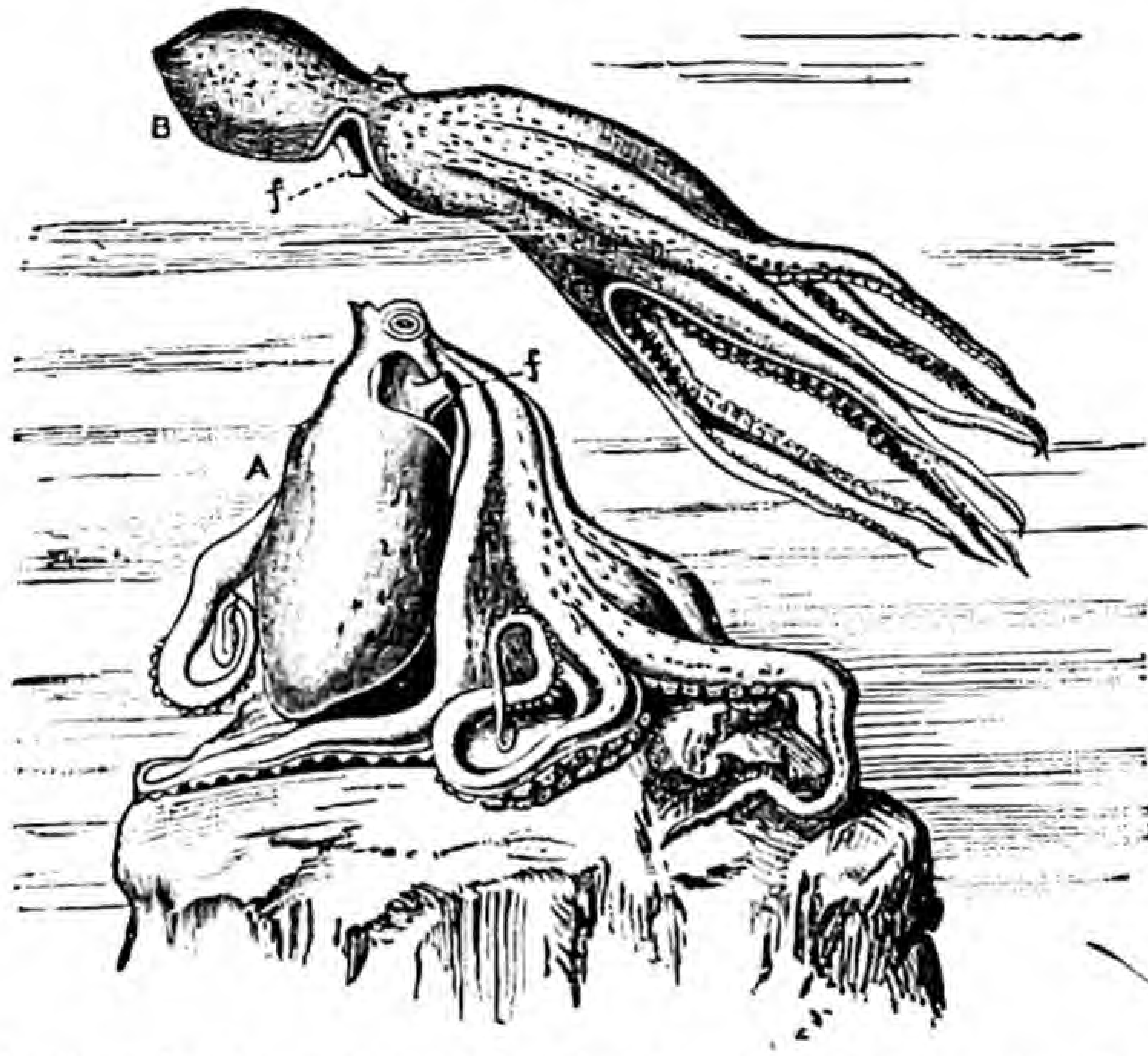


Fig. 643.—**Octopus vulgaris.** *A*, at rest; *B*, in motion. *f*. funnel, the arrow showing the direction of the propelling current through the water. (From Cooke, after Merculiano.)

propulsion of a current of water forcibly ejected through the funnel by the contraction of the muscular mantle (Fig. 643). When fins are present they may take the form of a continuous lateral flap as in Sepia, but, more usually, are of the nature of flattened lobes situated towards the aboral extremity of the body (Fig. 644); in *Ctenopteryx* they have the character of fringes of filaments. The arms vary in length and proportions and in the form and arrangement of the suckers. Eight arms are present in the Octopoda and ten in the Decapoda. In the former group the Argonauts (Fig. 645) have, in the female, one pair of arms flattened and expanded at the extremities for the secretion and support of the shell. In the Decapoda one pair of arms, the fourth, is always specially modified, as in Sepia, to act as prehensile

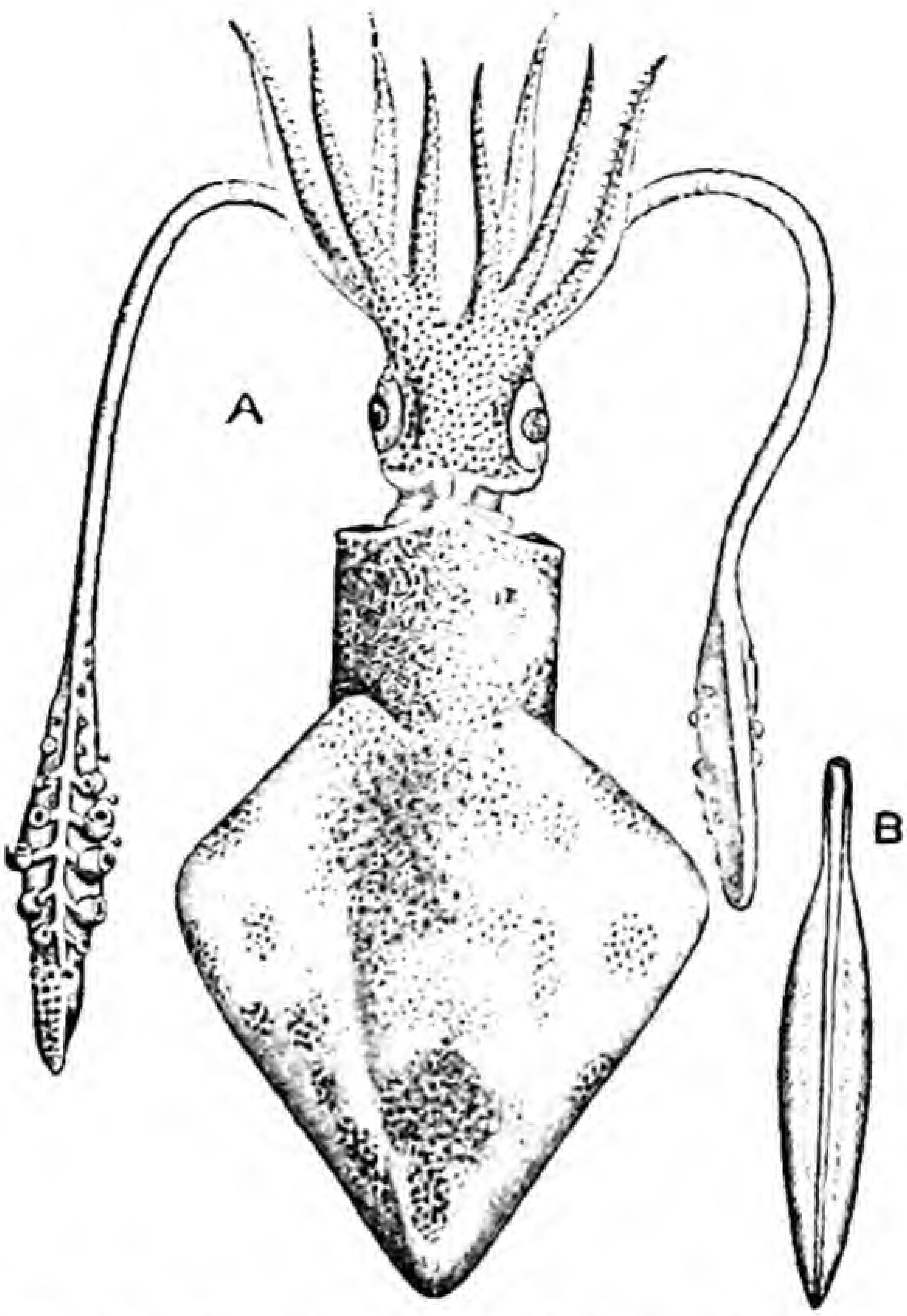


Fig. 644.—**Loligo vulgaris.** *A*, entire animal, dorsal view; *B*, horny internal shell or pen. (From Keferstein.)

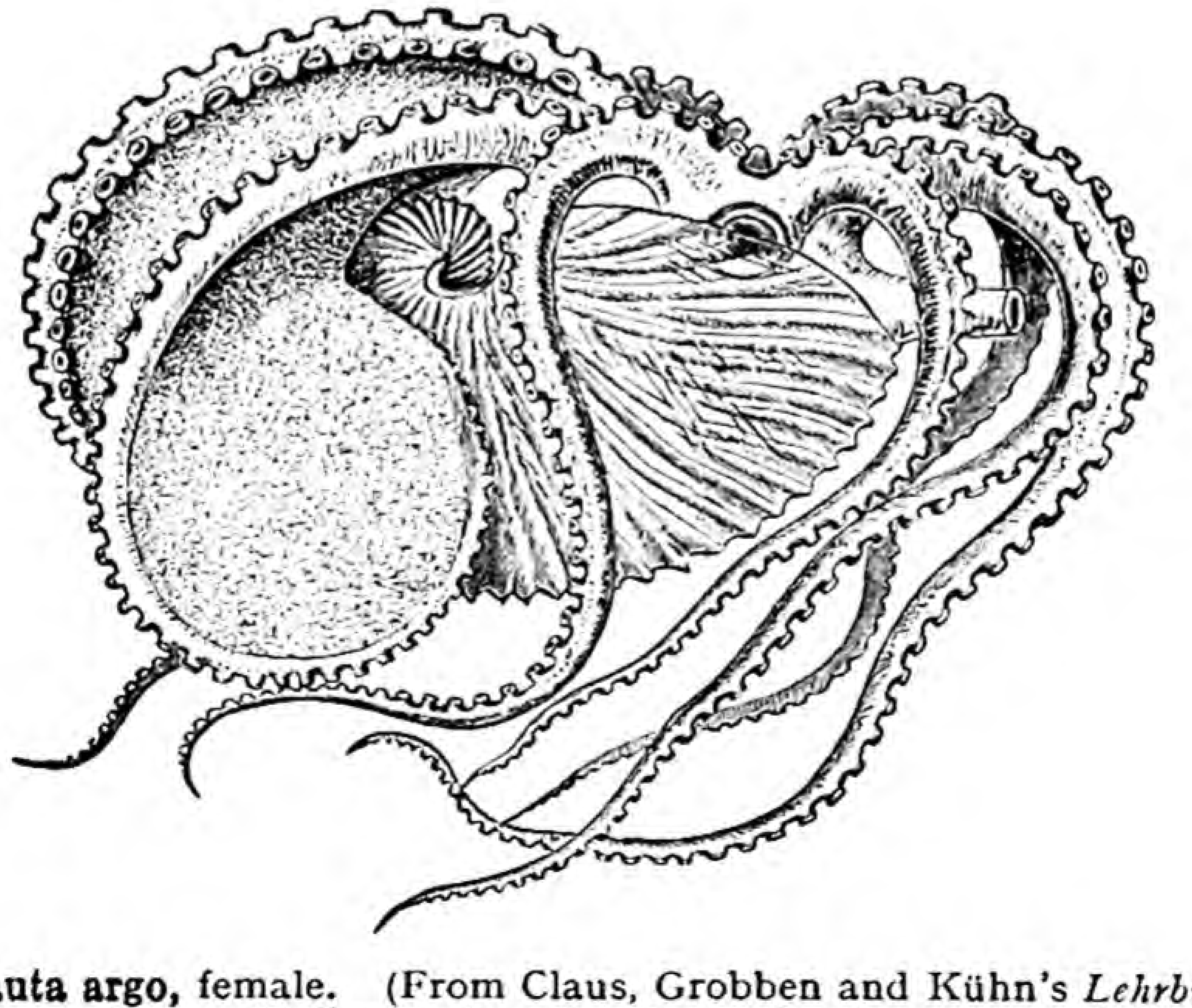


Fig. 645.—**Argonauta argo,** female. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Brehm.)

appendages or *tentacles* usually capable of being partly or entirely retracted within certain sacs situated at their bases. In nearly all one of the arms in the male is specially modified (or *hectocotylized*) to act as an intromittent organ. This modification is only very slight in Sepia and confined to the base, and is

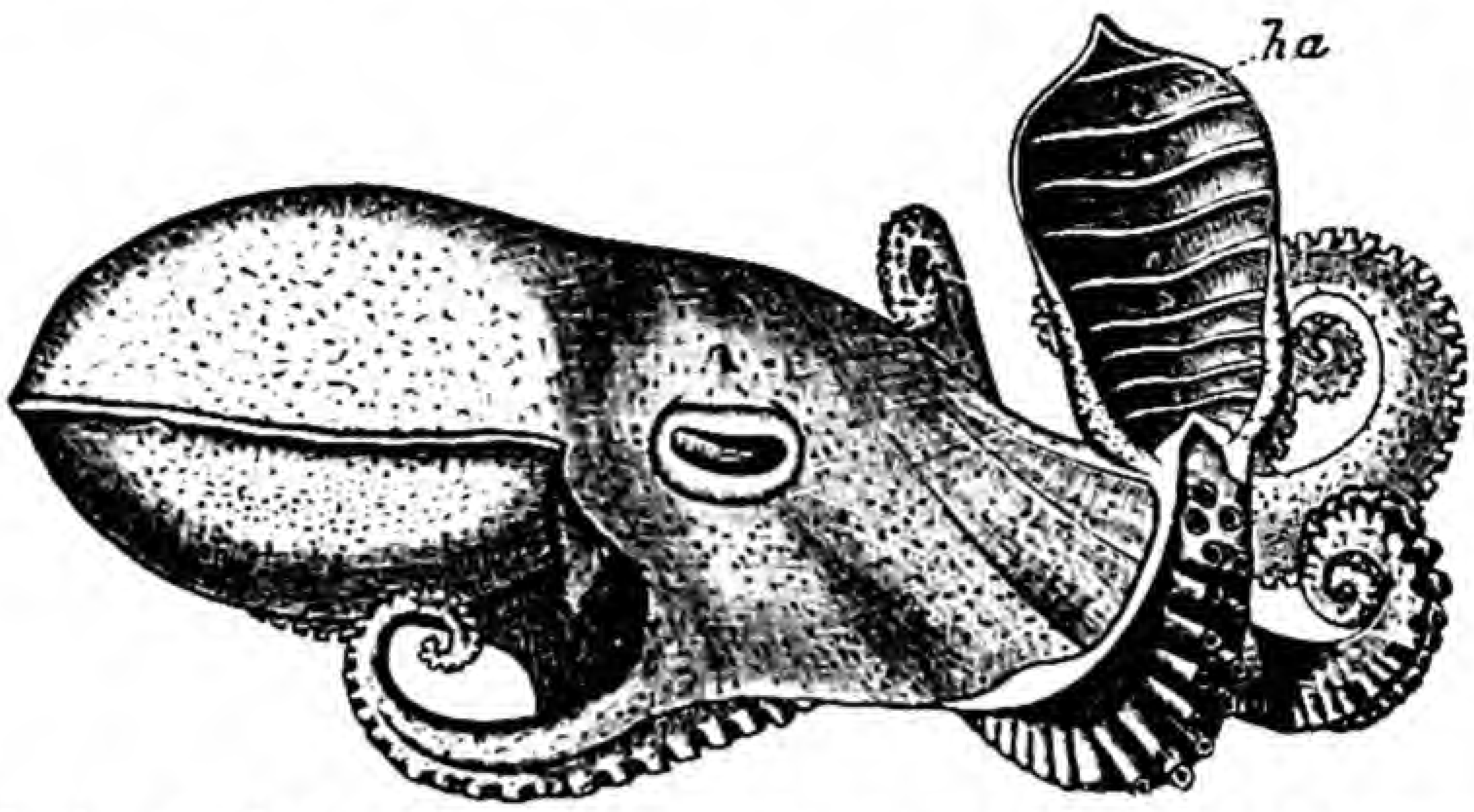


FIG. 646.—**Octopus lentus**, male specimen, showing the structure of the hectocotylized arm (*h. a.*). (From Cooke, after Verrill.)

most marked in certain of the Octopoda (Fig. 646, *h. a.*), including the Argonauts. In the latter, before the breeding season, the third arm in the male is found to be represented by a rounded sac, which subsequently bursts and sets free the elongated hectocotylized arm. Spermatophores are taken by the arm from the genital opening, and in the act of copulation the entire arm is detached and left in the mantle-cavity of the female. In other cases the arm is not detached. The suckers are sometimes stalked, sometimes sessile, sometimes armed with hooks, sometimes replaced by hooks. In many cases the arms are united by a web-like fold, the *interbrachial membrane* (Fig. 647) which may reach nearly to their extremities.

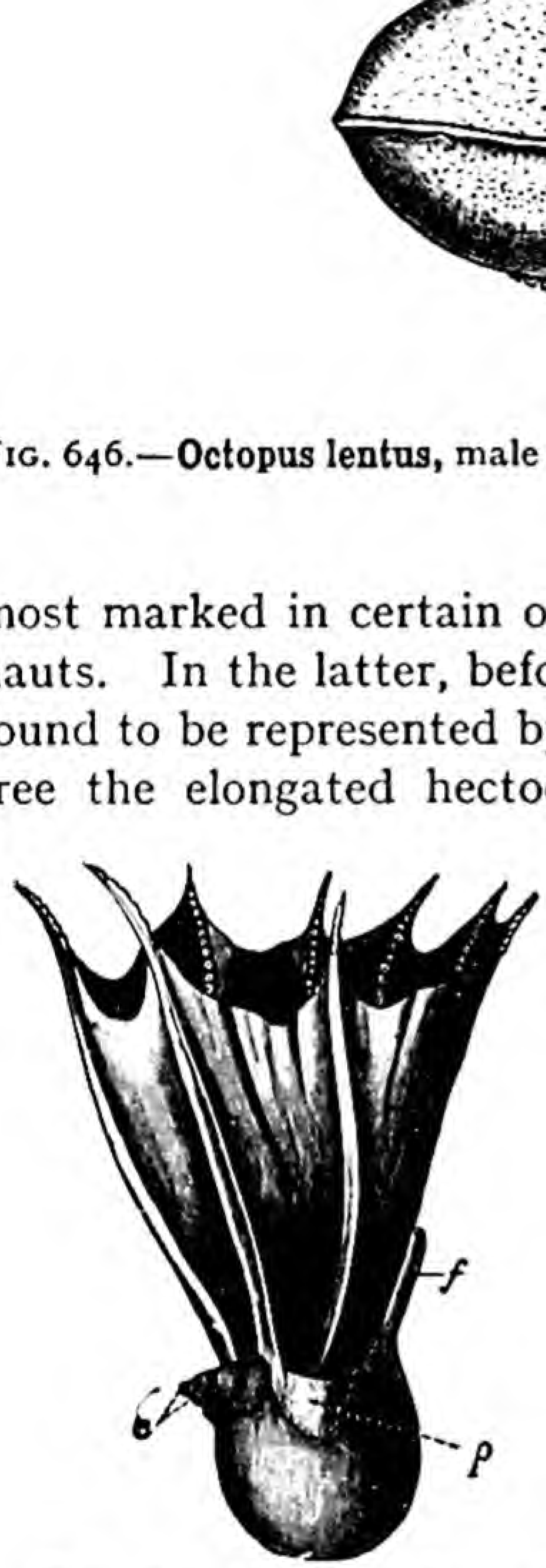


FIG. 647.—**Amphitretus pelagicus**, an Octopod with the arms united by a web. *e.* eyes; *f.* funnel; *p.* pouch in the mantle. (From Cooke, after Hoyle.)

In the Recent Nautiloidea the series of groups of slender, ringed, sheathed tentacles, situated on lobes of the foot surrounding the mouth, take the place of the arms, and suckers are not present. In the males the spadix probably represents, functionally at least, the hectocotylized arm of the Recent Belemnoidea.

In all the Recent Belemnoidea the *funnel* is a complete tube. In the Nautilus, on the other hand, as we have seen, the folds which form the funnel have their edges merely in apposition, and not united. A valve, such as has been described in Sepia, occurs in most Decapoda

and in Nautilus, but is absent in the Octopoda. *Chromatophores*, similar to those of Sepia, are universal in the Recent Belemnoidea but absent in Nautilus.

Shell.—The shell of Nautilus is the most complete and yet in a certain sense the most primitive. As already stated, it is an external shell of a spiral character, divided internally by septa into a series of chambers. The last of the chambers is occupied by the body of the animal; the rest are filled with gas. Perforating the middle of all the septa in succession is a spiral tube—the *siphuncle*—continuous with the centro-dorsal region of the visceral prominence. In the course of its growth the body of the Nautilus shifts forward at intervals into a newly-formed chamber, and a new septum is formed closing the latter

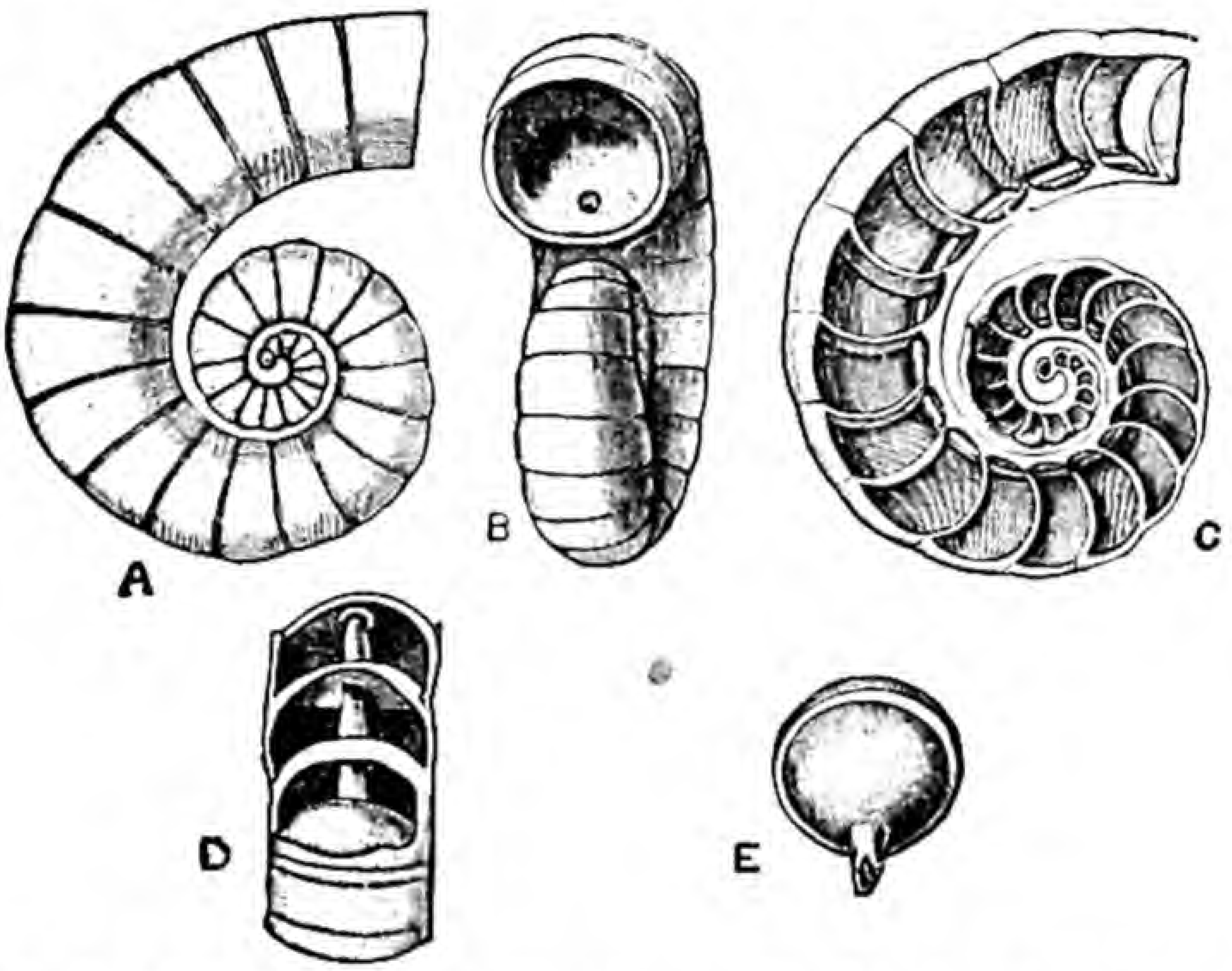


FIG. 648.—Shell of **Spirula**. *A*, outside view; *B*, showing last chamber and position of siphuncle; *C*, in section, showing the septa and the course of the siphuncle; *D*, shell broken to show the convexity of the inner side of the septa; *E*, portion of a septal neck. (After Cooke.)

off from the cavity last occupied. It is only after the last septum has been formed that the animal attains sexual maturity.

Of existing Belemnoidea, *Spirula* alone has a shell (Fig. 648) comparable to that of Nautilus. The shell of Spirula is of spiral form, the turns of the spiral, however, not being in contact. Internally it is divided into chambers by a series of septa, and these are perforated by a siphuncle. But the initial chamber (*protoconch*), instead of being, like the initial chamber in Nautilus, similar to the others though smaller, is dilated into a spherical shape, constricted off from the succeeding chamber, and has passing through it a tube—the *prosiphon*—not continuous with the siphuncle. The relation of the soft parts to the shell is the reverse of what obtains in Nautilus, the shell of Spirula curving backwards (*endogastric* curvature), that of Nautilus forwards (*exogastric* curvature). Moreover the shell of Spirula is an internal structure, being almost completely covered by the mantle.

The shell of the extinct Ammonoidea (Fig. 650), which may, or may not, have been tetrabranchiate, resembles that of the Nautilus in many respects, being a chambered spiral shell with a large terminal chamber, and with a siphuncle. The chief external difference is in the form of the *sutures*, or line of union of the edges of the septa with the side wall of the shell; these are more or less complexly lobed, instead of being entire as in Nautilus. But in one important respect the shell of an Ammonoid differs from that of Nautilus and approaches that of the dibranchiate Spirula. At the apex of the spiral is an initial chamber or protoconch, which is dilated and separated from the

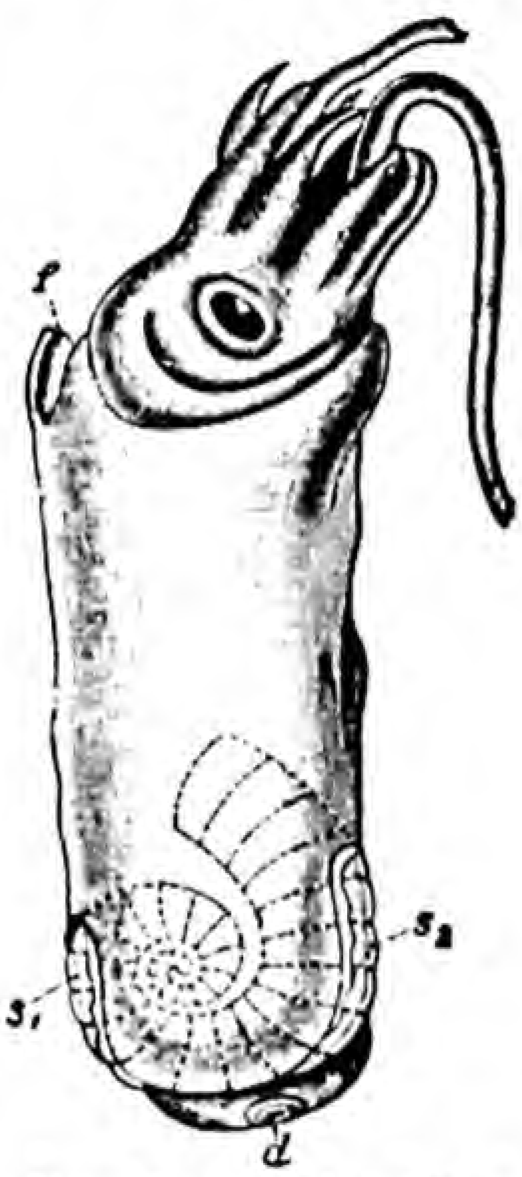


FIG. 649.—**Spirula peronii**, lateral view. *d.* terminal sucker; *f.* funnel; s_1, s_2. projecting portions of the shell, the internal part of which is indicated by dotted lines. (From Cooke.)

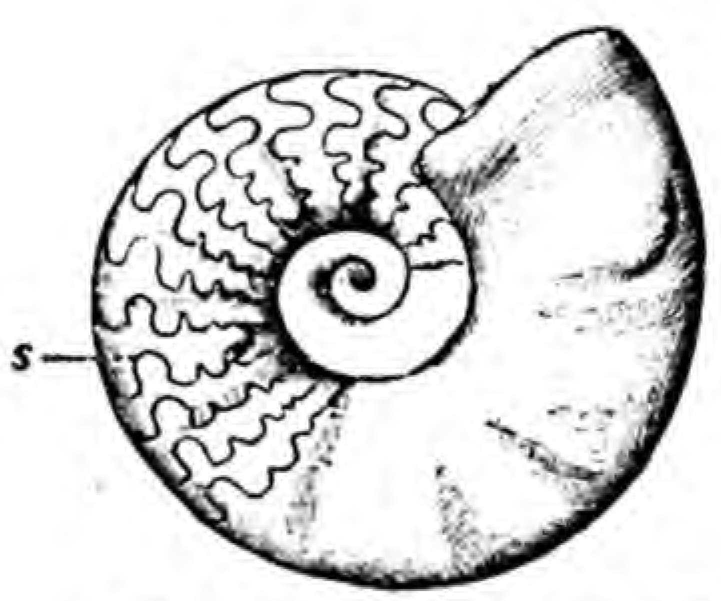


FIG. 650.—An **Ammonite** (*Ceratites nodosus*). *s.* lobed sutures.

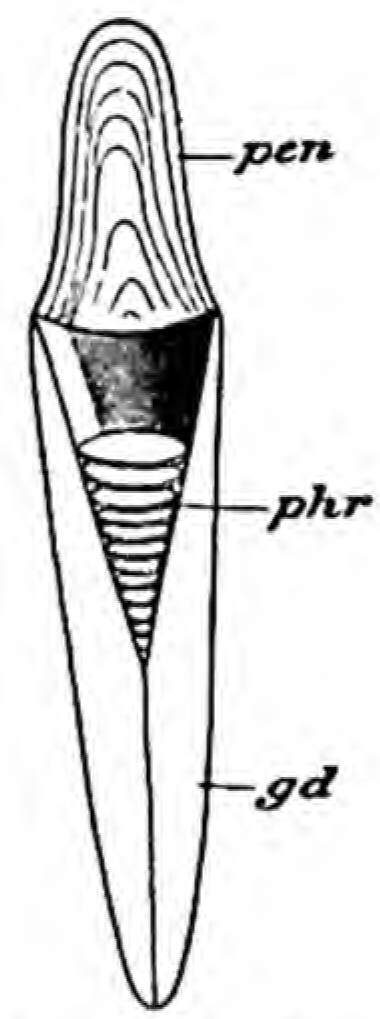


FIG. 651.—Shell of a **Belemnite.** *gd.* guard; *pen.* pro-ostracum; *phr.* phragmocone. (From Nicholson and Lydekker's *Palæontology.*)

first of the ordinary chambers by a constriction, and has passing into it a prosiphon not continuous with the siphuncle. The Ammonite was also characterized by the possession of a paired or unpaired calcified structure, called the *aptychus*, not represented in any existing form. The aptychus was most probably endoskeletal. Young Ammonites, each with its aptychus, have been found within the shell of the parent, in which they must have remained protected during their development.

In the ordinary decapod Belemnoidea the shell may consist of three parts—a horny *pen* or *pro-ostracum*, a calcareous *guard*, and a part termed the *phragmacone*. The last, which alone represents the shell of *Spirula*, has the form of a cone divided internally by a series of septa perforated by a siphuncle. These parts are most completely developed in the extinct genus Belemnites, in which

the shell (Fig. 651) consists of a straight, conical, chambered phragmacone (*phr.*), with a siphuncle, enclosed in a calcareous sheath, the guard, produced into a horny or calcareous plate, the pro-ostracum (*pen.*). In Sepia the spine-like projecting point represents the guard, and the main substance of the shell is to be looked upon as the pro-ostracum and phragmacone. In the Squids (*e.g.*, *Loligo*) the shell (Fig. 644, *B*) is long, narrow, and completely horny; it corresponds to the pro-ostracum, the phragmacone being entirely absent.

In *Octopus* the shell is represented only by a pair of vestiges with which muscles are connected. In *Argonauta* there is no shell in the male, but the female has an external shell (Fig. 652) of a remarkable character. This is a delicate spiral structure the internal cavity of which is not divided into chambers. It is not secreted by the mantle like the shells of other Mollusca, but by the surfaces of a pair of the arms ending in expanded disc-like extremities,

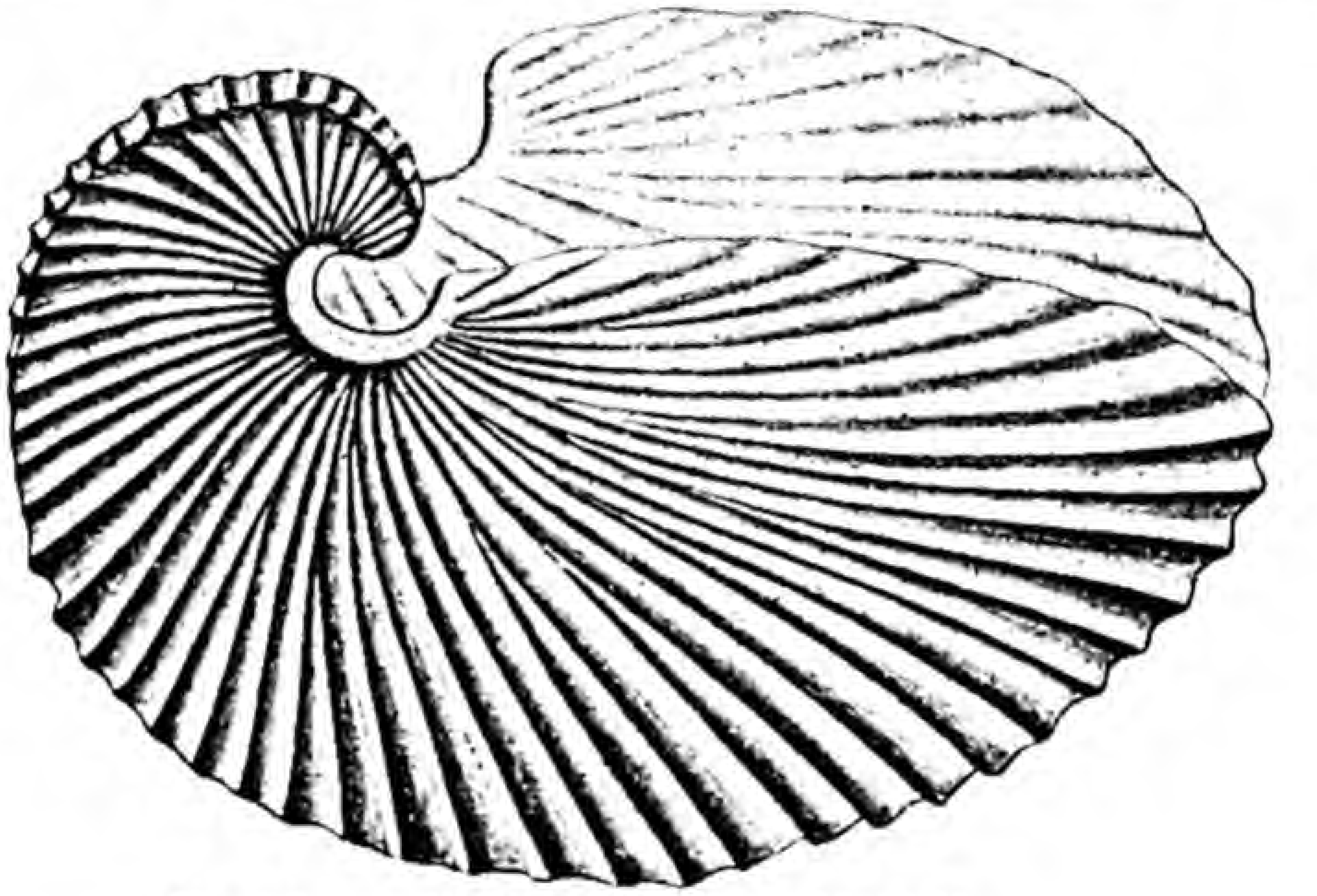


FIG. 652.—Shell of **Argonauta argo**.

which become applied to its outer surface (Fig. 645); its chief function is to carry the eggs.

An **internal cartilaginous skeleton** is present not only in Sepia and Nautilus, as already described, but in all the Cephalopoda. Such an internal skeleton occurs in other groups—some Chætopoda, Crustacea, and Arachnida—but attains a much more elaborate character in the present group than in any other Invertebrates.

The plume-shaped **gills**, lodged in the mantle-cavity, are two in number in all the Recent Belemnoidea, as in Sepia. In the Recent Nautiloidea there are four gills, similar in general character to those of the Recent Belemnoidea.

The **cœlome** in the Recent Belemnoidea has the extent already indicated in the case of Sepia, except that in the Octopoda the oral part does not exist. In Nautilus it encloses, besides the heart and gonad, a part of the glandular appendages of the afferent branchial vessels. In the Recent Belemnoidea the pericardial portion communicates with the renal sacs; in Nautilus this com-

munication is absent, but the cœlome opens on the exterior by two symmetrical viscero-pericardial orifices placed at the side of the openings of the aboral kidneys.

Alimentary Organs.—Jaws similar to those of *Sepia* are present in all the members of the class; in Nautilus, instead of being completely horny, they are partly calcified. Buccal mass, œsophagus, stomach, intestine, salivary glands, and digestive gland are all of the same general character throughout all the members of the class. In some of the Recent Belemnoidea, such as Octopus, there are two pairs of salivary glands. In Nautilus the salivary glands are absent, so far as known, the œsophagus is dilated to form a sort of crop, and the stomach is gizzard-like. In that genus also the ink-gland, general in the Recent Belemnoidea, is absent, and there is a cæcal appendage to the intestine; the digestive gland is four-lobed, each lobe having its duct. The so-called pancreas, described in Sepia, is similarly developed in all the Recent Belemnoidea, and is present also, though only feebly developed, in the Recent Nautiloidea.

Heart and **vascular system** are well developed in the Cephalopoda, and their structure and arrangement closely correspond with what has been described in Sepia, except that in Nautiloidea there are, as already stated, in accordance with the double number of gills, four auricles instead of two, and branchial hearts are absent.

Nervous System and Sense-organs.—The ganglia of the central nervous system are in all closely aggregated together round the œsophagus, as already stated to be the case in Sepia; and the general disposition is the same as that described. In Octopus the ganglia are much less sharply marked off. In Nautilus, as already mentioned, there is less concentration, and distinct ganglia are not recognizable. All the Recent Belemnoidea possess highly developed *eyes* similar to those of Sepia, elevated on stalks in certain cases; but in Nautilus the eyes are of a much simpler character, each consisting of a sac opening on the exterior by a small rounded aperture, lined internally by a two-layered retina similar to that of Sepia, but without lens, vitreous humour, or cornea. In the embryo of the Recent Belemnoidea, the eye passes through a stage in which it is in the condition of an open cup similar to the adult eye of Nautilus. *Osphradia* are present, as already mentioned, only in the Recent Nautiloidea; but in both the Recent Nautiloidea and the Recent Belemnoidea certain sensory processes or depressions conjectured to possess an olfactory function are developed on the head. *Statocysts* are universally present.

All the Recent Belemnoidea have two **kidneys** or **renal sacs** similar in character to those of Sepia, and communicating with one another; in Octopus they are completely united. In the Recent Nautiloidea there are four kidneys, each opening on the exterior.

The **sexes** are distinct in all the Cephalopoda, and in addition to the hecto-

cotylized arm there are frequently other external differences between male and female. In all the Recent Belemnoidea the arrangement of the gonads and gonoducts is, as regards general features, similar to what we find in Sepia. In Octopus, however, there are two oviducts instead of one, and in one other member of the Octopoda (*Eledone moschata*) the same holds good of the spermiducts.

Development.—The embryonic development of the Recent Belemnoidea is known, but not that of the Nautiloidea. The eggs are very large, containing a relatively large amount of food-yolk. They are usually laid in masses or strings embedded in a soft, gelatinous, or a tougher, more leathery substance, usually attached to some foreign body; in some cases each egg, enclosed in a gelatinous sheath, has a longer or shorter stalk. A *chorion* or delicate transparent egg-membrane, in which there is an aperture—the *micropyle*—immediately invests the egg itself. In shape the egg is oval or spherical. The greater part of the comparatively small quantity of protoplasm lies as a disc-like elevation on the surface of the yolk on the side of the egg at which the micropyle is situated. Continuous with this *germinal disc* is a thin layer of peripheral protoplasm investing the entire ovum.

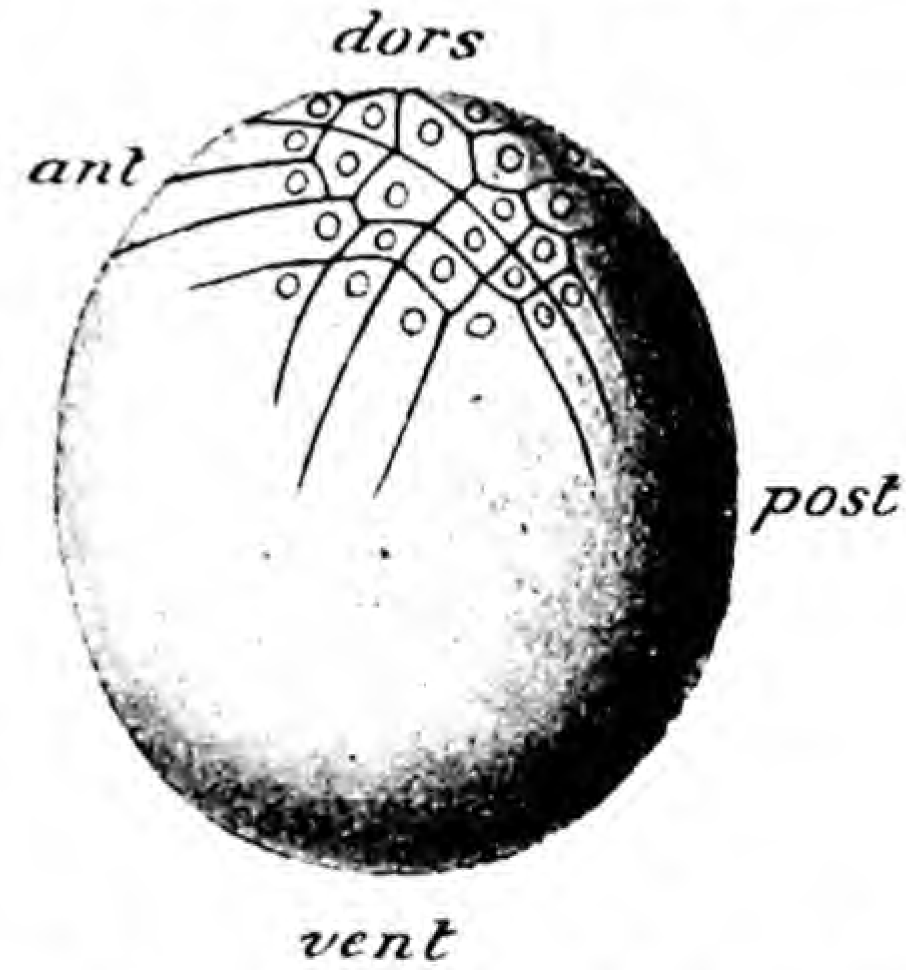


FIG. 653.—Cleaving ovum of **Loligo.** (From Korschelt and Heider, after Watasé.)

Cleavage (Figs. 653 and 654) is incomplete, being confined to the germinal disc. At an early stage in the process of division the blastoderm exhibits a distinct bilateral symmetry. The meroblastic cleavage results in the formation of a nearly circular blastoderm, the outer cells of which tend to separate off. At first the blastoderm consists of only a single layer of cells—the ectoderm which gradually extends. At a later stage a second layer (Fig. 655, *B*, *C*) appears below the margin of the blastoderm and extends inwards until it comes to underlie the greater part of the embryonic part of the blastoderm: separating this from the yolk is a thin layer of uncertain derivation—the *yolk-epithelium* (Fig. 655, *yk. ep.*). There is some doubt as to the nature of the second layer; it certainly gives rise to the mesodermal structures, and by some observers it is also said to form the epithelium of the mesenteron. From whatever source it may be derived, the latter becomes distinguishable as a cell-plate which becomes converted into a vesicle at first opening below against the yolk epithelium, there never being any direct communication with the yolk. An extensive stomodæum eventually opens into this; a proctodæum is merely represented by the ectodermal pit forming the anus.

About the middle of the blastoderm appears a thickening of a cap-like shape, the edges of which become raised above the general level of the blastoderm ; this is the rudiment of the mantle. On the surface of this is developed

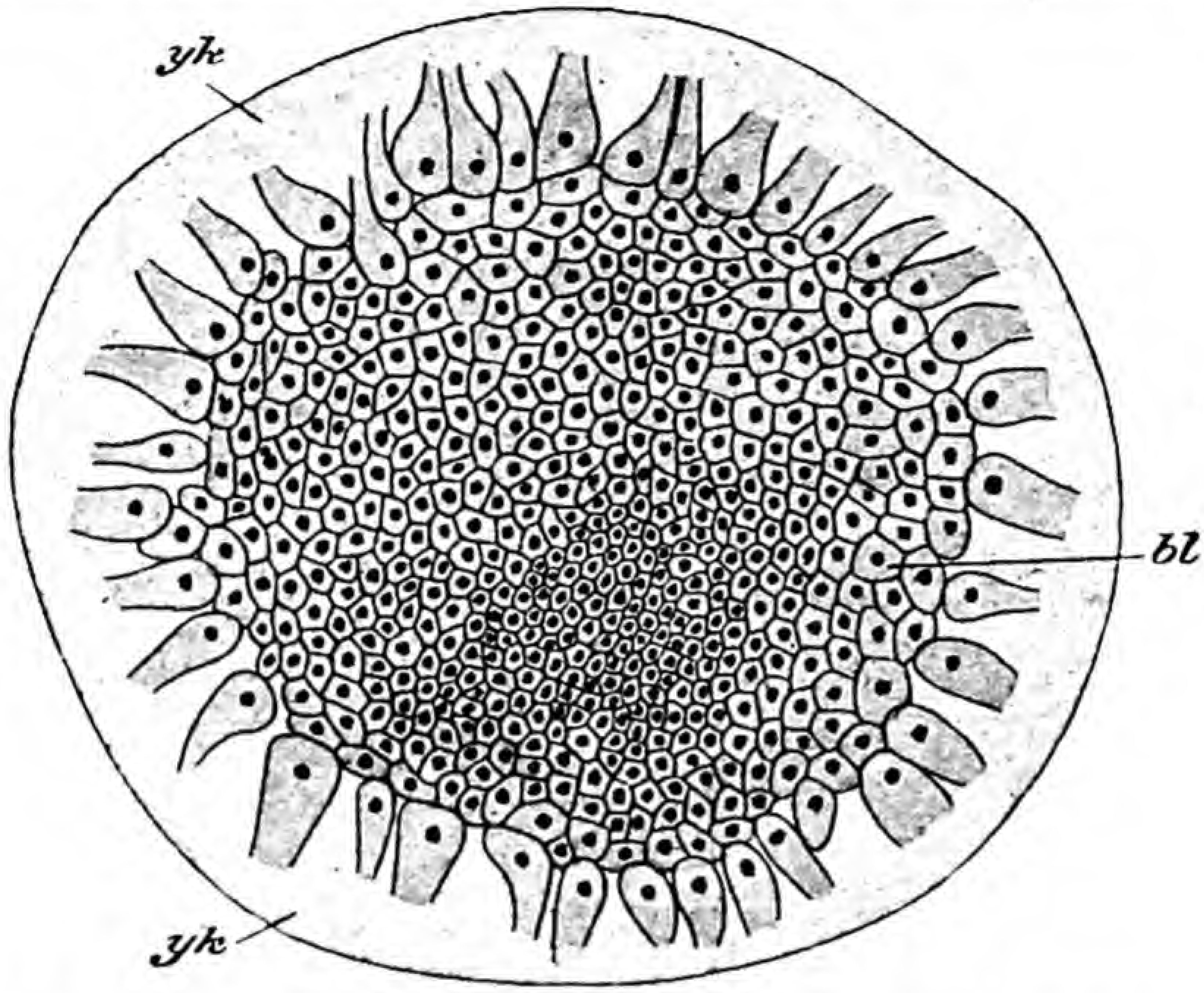


FIG. 654.—**Sepia,** blastoderm at a late stage of cleavage. *bl.* blastoderm ; *yk.* yolk. (From Korschelt and Heider, after Vialleton.)

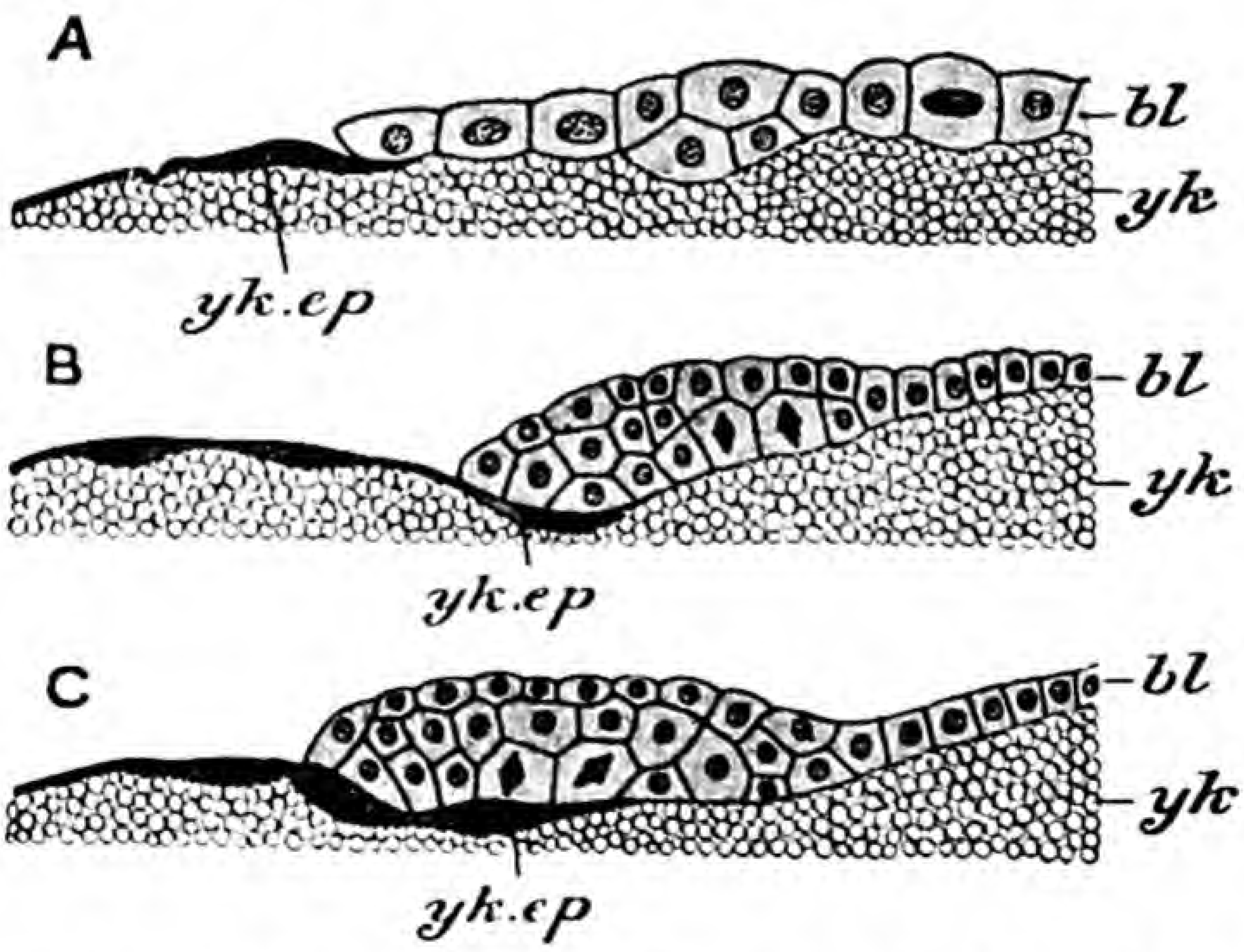


FIG. 655.—Sections through the edge of the blastoderm of **Sepia** at three successive stages. *bl.* blastoderm ; *yk.* yolk ; *yk. ep.* yolk-epithelium. (From Korschelt and Heider, after Vialleton.)

a depression which subsequently forms a closed sac—the *shell-gland* (Fig. 656, *sh. gl.*). Below the mantle—*i.e.*, nearer the vegetative pole—appear two elevations, each with a pit-like depression, which are the rudiments of the eyes ;

and still nearer the vegetative pole a series of paired elevations, the rudiments of the arms.

After the complete enclosure of the yolk by the blastoderm, the mouth (*mo.*) is developed as an oval depression between the rudiments of the eyes. Immediately in front of the edge of the mantle appear two short ridges, the

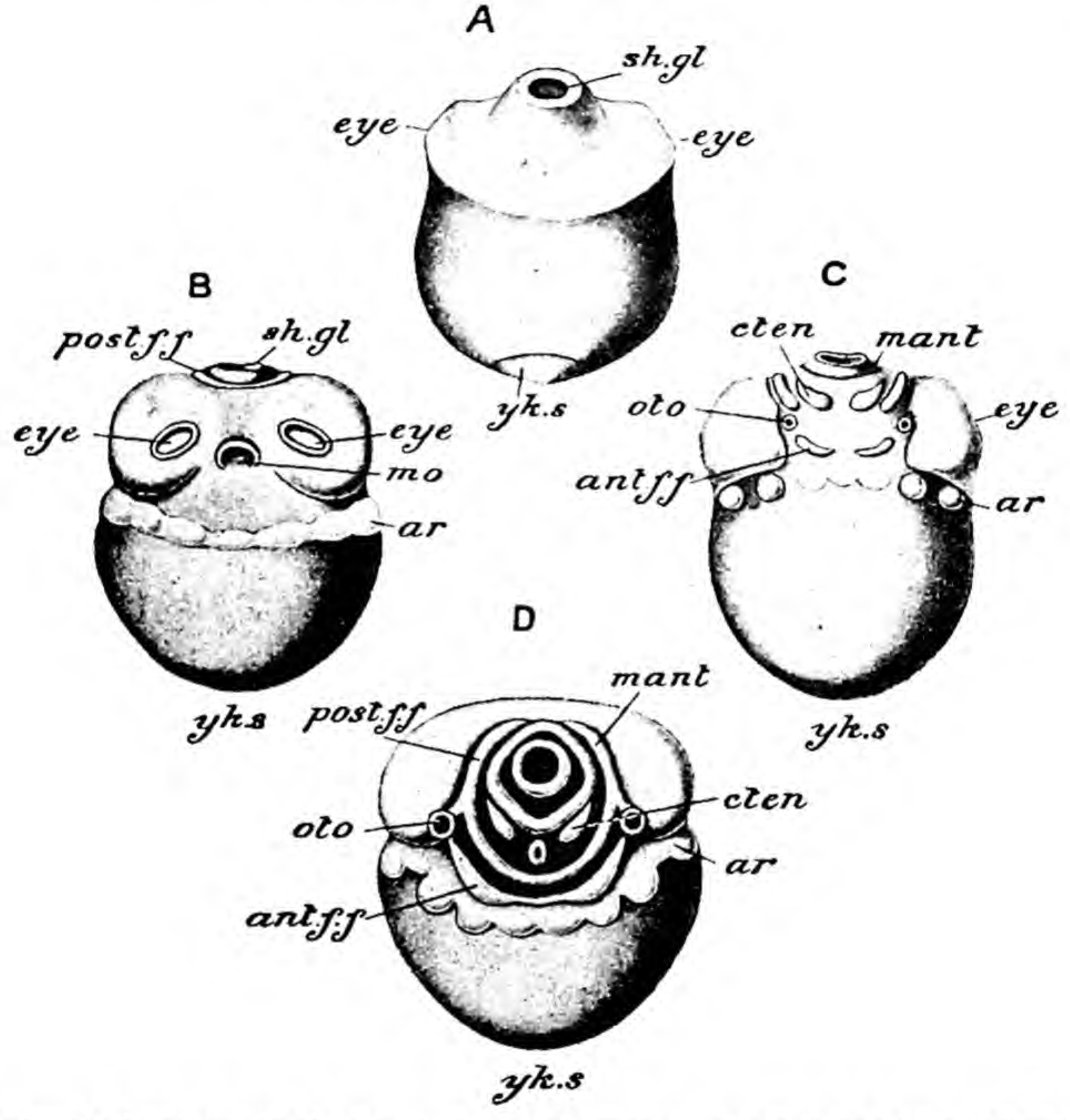


FIG. 656.—Early stages in the development of **Loligo.** *A*, stage at which the rudiments of the eyes and of the shell-gland are first distinguishable; *B*, later embryo from the oral side; *C* and *D*, from the anal side. *ant. f. f.* anterior funnel fold; *ar.* rudiments of arms; *cten.* ctenidia; *eye*, eye; *mo.* mouth; *mant.* rudiment of mantle; *oto.* statocyst; *post. f. f.* posterior funnel fold; *sh. gl.* shell-gland; *yk. s.* yolk-sac. (After Korschelt and Heider.)

beginnings of the gills (*cten.*), and a pair of folds—the *posterior funnel-folds* (*post f. f.*)—which are formed between these and the eyes, are the first rudiments of the funnel; the greater part of which, however, is formed from a second pair of folds—the *anterior funnel-folds* (*ant. f. f.*)—developed farther forwards. Behind the anterior funnel-folds appear two pit-like depressions, which subsequently develop into the statocysts.

The elevations on which the eyes (*eye*) are situated become more and more prominent. The eyes themselves are formed from a part only of these eleva-

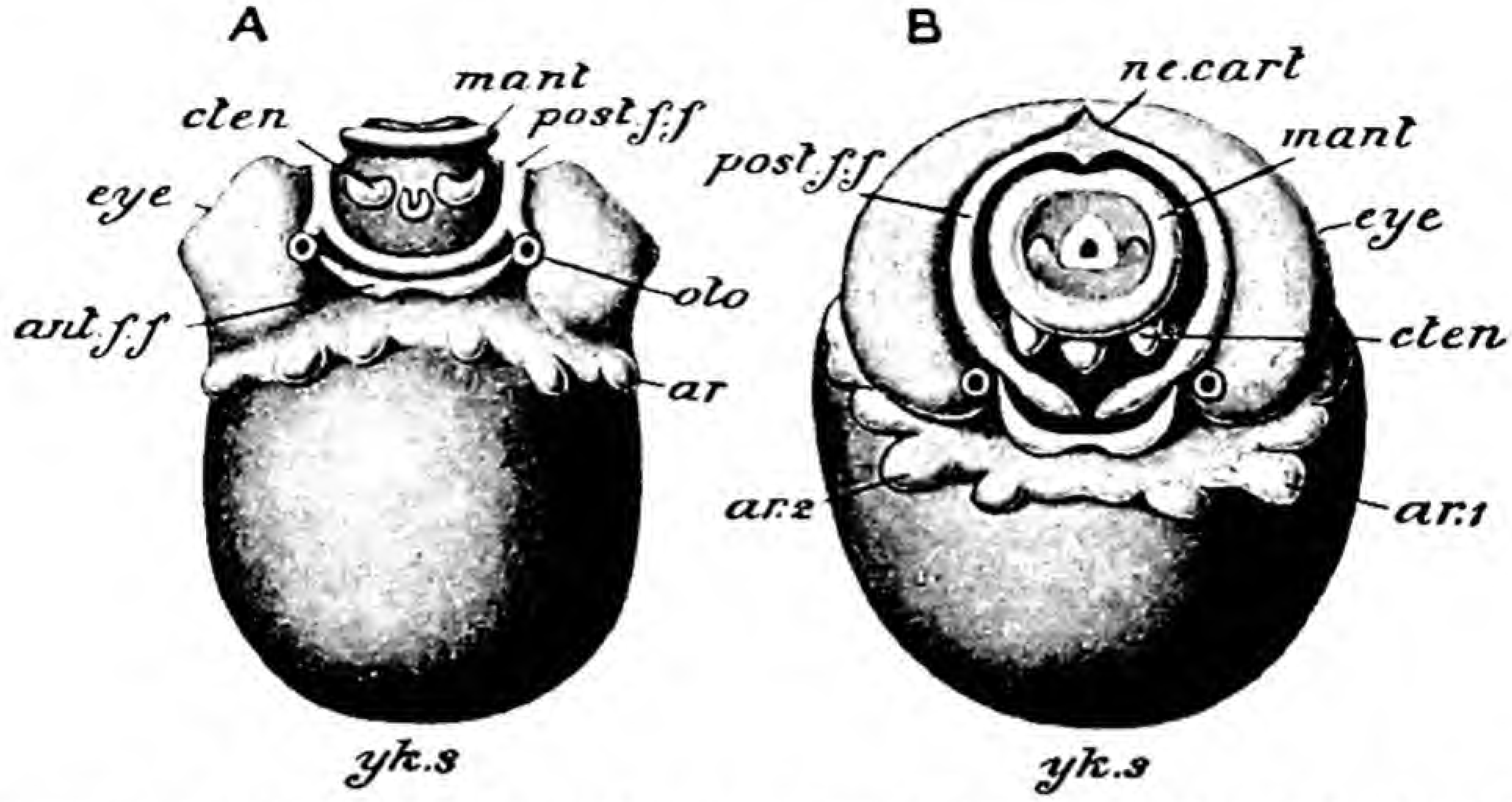


FIG. 657.—Two later stages in the development of **Loligo.** *A*, from the funnel side; *B*, obliquely from above. Letters as in preceding figures; *ne. cart.* nuchal cartilage. (After Korschelt and Heider.)

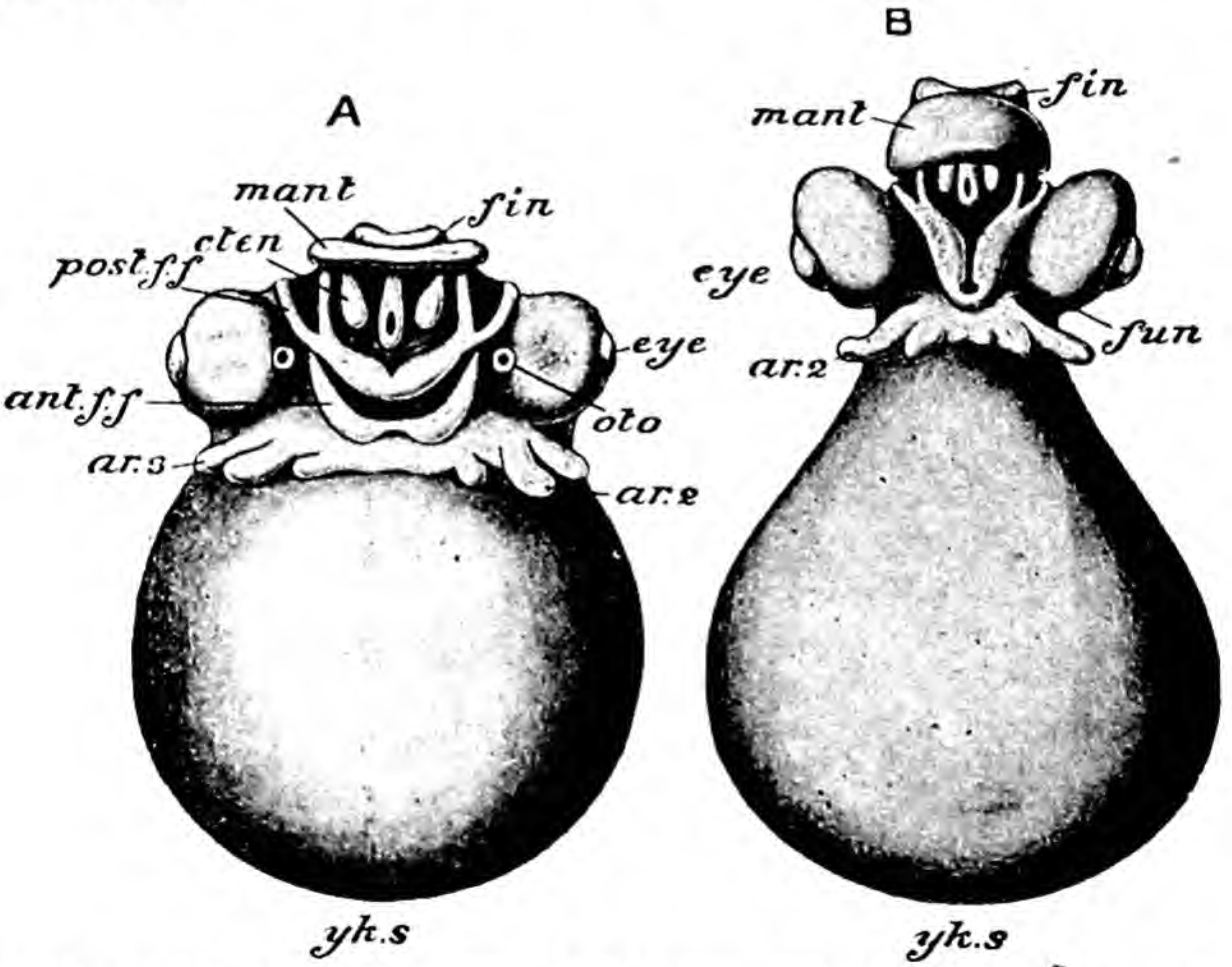


FIG. 658.—Two stages in the development of **Loligo,** later than those represented in Fig. 657. From the anal or funnel side. Letters as in preceding figure; in addition, ***fin***, fins; ***fun***. funnel. (After Korschelt and Heider.)

tions; each is a pit which subsequently becomes closed to form a vesicle—the *optic vesicle*: later an ingrowth of the ectoderm over this gives rise to the lens.

The embryo covers only a part of the egg, and as it develops, it withdraws

itself more towards the animal pole, at which the germinal disc was originally situated—a constriction, which soon becomes very deep, separating it off from the rest of the egg; the latter, consisting of the greater part of the yolk enclosed in a thin layer of blastoderm, forms a rounded appendage of the embryo—the *yolk-sac* (*yk. s.*). The yolk-sac undergoes contractions, which are due to the action of contractile cells in the thin mesoderm lining it, and by this means the yolk is forced into the interior of the body of the embryo.

The anus appears as an aperture situated on a little papilla—the *anal*

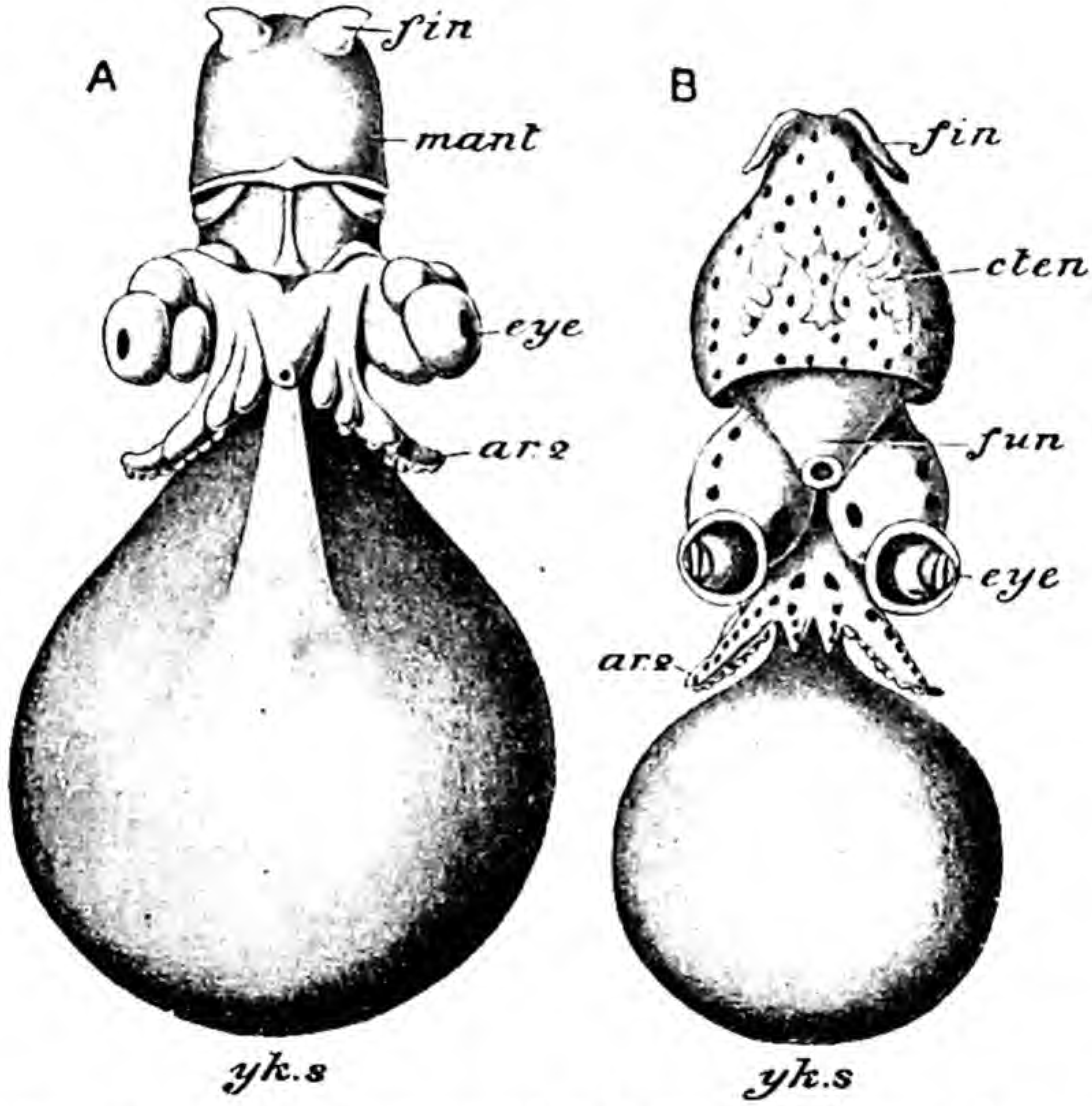


FIG. 659.—Two late stages in the development of **Loligo**, seen from the funnel side. Letters as in preceding figures. (After Korschelt and Heider.)

papilla. A row of cilia, which are developed in the neighbourhood of the mouth in some forms, perhaps represent the velum or pre-oral circlet of other molluscan embryos. The mantle now increases in extent, and its margins become more prominent. The anterior funnel-folds grow out and unite in the middle line; and these, with the posterior folds, go to form the completed funnel together with the "neck-muscles." For a time the edges of the two folds which form the funnel remain free; eventually they coalesce into a complete tube.

The edges of the mantle grow out into prominent folds to form the mantle-cavity, into which the gills are drawn. Lateral outgrowths have already given

rise to the rudiments of the fins. The arms grow out into more and more prominent processes on which the suckers are developed, the fourth pair—the prehensile arms (*ar. 2*)—soon becoming distinguishable from the rest by their greater length.

As the embryo increases in size, the yolk is gradually absorbed, and the yolk-sac decreases in bulk, until, when the embryo leaves the egg, it has almost completely disappeared.

Distribution.—The Cephalopoda are all marine, and range from tidal limits to a considerable depth. A large number (*Loligo*, etc.) are pelagic and move together in great shoals. Sepia lives chiefly between stones and in rock-fissures in the littoral zone, and often burrows in sand. Octopus constructs a den or shelter of stones to which it always returns after excursions in search of food. Cephalopods are, nearly without exception, carnivorous. In length they range from an inch or two to as much as fifty feet—the gigantic members of the group, such as *Architeuthis*, being by a long way the largest of invertebrate animals. Like the other classes of Mollusca they are most abundant in tropical and warm-temperate seas.

The Ammonoidea were most abundantly represented during the Mesozoic period; while the Nautiloidea were most abundant in the Palæozoic epoch, during which there lived a great variety of forms of this group, the shell being straight (*Orthoceras*), or curved (*Phragmoceras*), or in a flat spiral with the turns not in contact, or in a helix, or a flat close spiral (*Nautilus* and others). The earliest representatives of the Nautiloids are found in rocks of Cambrian age; they are comparatively scarce in the Mesozoic epoch and in the Tertiary, and are represented at the present day only by the genus *Nautilus* itself. The Ammonoids are mainly Mesozoic, the representatives found in the earlier rocks (from the Devonian onwards) being few in number and simpler in structure than the more typical later forms. The oldest fossil representatives of undoubted Belemnoidea belong to the extinct order of the Belemnites, which flourished in the Mesozoic period from the Trias to the Cretaceous, and survived in scanty number into the Tertiary. Unlike the Nautiloidea and Ammonoidea, the Belemnoidea would appear to have reached their maximum at the present day.

General Remarks on the Mollusca.

The Mollusca, like the Arthropoda, form an extremely well-defined phylum, none of the adult members of which approaches the lower groups of animals in any marked degree. There are, however, clear indications of affinity with "Worms," especially in the frequent occurrence of a trochophore stage in development, and in the occurrence, in the Solenogastres, Placophora, and some of the lower Gastropoda, of a ladder-like nervous system resembling that of some Turbellaria.

If the occurrence of the trochophore be taken as a guide towards the ancestry of the Mollusca, it need not necessarily be regarded as leading back to the Annelida. In fact the absence of segmental repetition of parts in all would seem to indicate the derivation of the phylum from a group in which metamerism had not arisen. It will be readily recognized that the gap between the typical trochophore and certain forms of turbellarian larvæ (Müller's larva) is not a very wide one, and might be covered by adaptation of the larval Flatworm to a freer pelagic life. If we were to suppose that the most primitive Mollusca were derived from turbellarian-like ancestors, the conversion of a larva of the type of Müller's larva into a larval form like the molluscan trochophore would also have to be postulated. This might involve a common platyhelminth origin for the Annelida and Mollusca, with subsequent extreme divergence—a divergence in which the respective trochophores would take part, though in a limited degree. The chief changes which the adult animal would have to undergo in order to assume the character of a primitive Mollusc on this supposition would be—(1) the development of some kind of protective layer of hard material, perhaps composed at first of spicules in a thickened integument, on the dorsal surface—the rudiment of the shell; (2) the greater development of the muscular layers of the body-wall on the ventral side to give rise to a more efficient and specialized creeping organ than was possessed by the turbellarian ancestor; (3) the development of specialized respiratory organs in the form of ctenidia—a change rendered necessary by the great reduction in the available respiratory area brought about by the development of the shell; (4) the formation of an anus and proctodæum; and (5) the development of a cœlome.

With regard to the relationships of the various classes of Mollusca, the following points are some of the most important to be borne in mind.

The simplest members of the phylum are undoubtedly the Solenogastres and the Protobranchiata among the Bivalvia. The former take the lowest rank in virtue of the absence of both foot and shell, but the possession by some of a radula indicates a comparatively high degree of specialization. On the other hand, while there is no indication of an odontophore, even in a rudimentary condition, in the Bivalvia, the foot and shell are well developed even in Nucula and its allies. There is no actual evidence to show that the foot and shell have been lost by degeneration in the Solenogastres or the odontophore in the Bivalvia; and it would appear, therefore, that the two groups are to be derived independently from some primitive form.

The facts that the bivalve shell, at its first appearance, is univalve, and that the foot of the Protobranchiata is of the creeping type and their ctenidia plume-like, suggest the derivation of the class from a form resembling a simple type of Gastropod with no odontophore and with undisturbed bilateral symmetry. The Solenogastres and the Placophora are also bilaterally symmetrical,

with paired ctenidia, kidneys, and auricles; and the fact that these organs are also paired in the lower Gastropoda seems to point to a common ancestor, which was bilaterally symmetrical, had a creeping foot, a simple shell, paired auricles, kidneys, and gills, and no odontophore.

While the leading feature in the evolution of the Bivalvia has been the splitting of the shell into two halves, the most noticeable fact in that of the Gastropoda, apart from the appearance of the odontophore, has been the torsion of the visceral mass, producing a characteristic asymmetry. In the Cephalopoda, on the other hand, the primitive bilateral symmetry is retained, and the most characteristic special feature of the group is the extraordinary modification of the foot into arms or tentacles, and funnel. The class is raised far above the remaining Mollusca by its wonderfully high organization, especially of the nervous system and the eye, and there is nothing to indicate close relationship with any of the lower classes beyond the general conformity to the molluscan plan of organization and the presence of an odontophore. The Cephalopods form, in fact, a singularly isolated group. Palæontology has not hitherto given any indication of their origin, and embryology is equally silent; the absence of a free larva, and the profound modification in development produced by the enormous mass of food-yolk, sharply separating them from all other members of the phylum.

SECTION X

In this section four classes of cœlomate animals: the *Bryozoa* (*Ectoprocta*), the *Phoronida*, the *Brachiopoda*, and the *Chætognatha* will be described. The first three are frequently held to constitute the phylum *Molluscoidea*. In view of their wide structural divergence and the absence of any conclusive evidence as to their mutual relationships, this mode of classification has here been abandoned. The inclusion in this section of the isolated class Chætognatha is to be considered a mere matter of convenience.

THE BRYOZOA (ECTOPROCTA).

The Bryozoa form colonies known as "Sea-mats," or "Corallines," which in many cases bear a close general resemblance to hydroid Cœlenterates, and only on a more minute inspection are found to differ totally from the latter and to exhibit a very much higher type of structure.

1. Example of the Class—*Bugula avicularia*.

Bugula avicularia, the common Bird's-Head Coralline (Fig 660), occurs in brown or purple bushy tufts, two or three inches long, on rocks, piles of jetties, and similar situations on the sea-shore in all parts of the world. On a naked-eye examination it presents a considerable resemblance to a hydroid Cœlenterate, and might readily be taken for a member of that group. It consists of dichotomously branching narrow stems, which are rooted by a number of slender root-filaments. Each stem is found, when examined with a lens, to be made up of a number of elements, the *zoœcia* of the colony, which are closely united together and arranged in four longitudinal rows. The zoœcia are approximately cylindrical in shape, but broader distally than proximally, four or five times as long as broad, and have, near the distal end, a wide crescentic aperture—the "*mouth*" of the zoœcium—on either side of which is a short blunt spine. A rounded structure—the *oœcium*—in many parts of the colony lies in front of each zoœcium (Fig. 660, *oœc.*). On each zoœcum, except a few at the extremities of the branches, is a remarkable appendage, the *avicularium* (*avic.*), having very much the appearance of a bird's head supported on a very short stalk; if the Bugula is examined under the microscope in the living condition, the avicularia will be found to be in almost constant movement, turning from side to side; and a movable part, comparable to the lower jaw of the bird's head, will often be

seen to be moved in such a way that the mouth of the avicularium is opened very widely and then becomes closed up with a quick "snap." All the parts

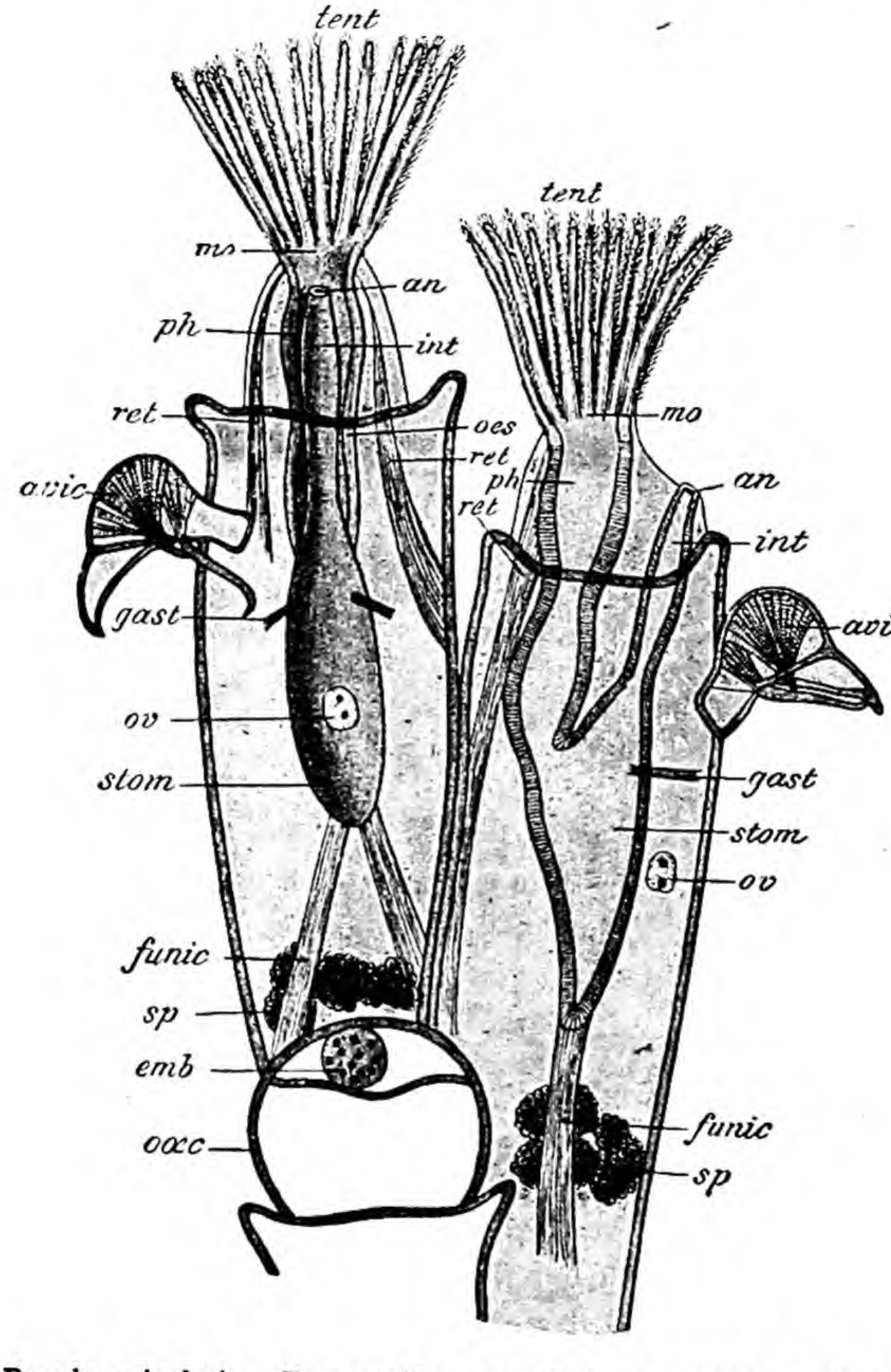


FIG. 660.—**Bugula avicularia.** Two zooids, magnified. *an.* anus; *avic.* avicularia; *emb.* embryo enclosed in the oœcium; *funic.* funiculus; *gast.* muscular bands passing from the stomach to the body-wall; *int.* intestine; *mo.* mouth; *oœc.* oœcium; *œs.* œsophagus; *ov.* ovary; *ph.* pharynx; *ret.* parieto-vaginal muscles; *sp.* spermatidia; *stom.* stomach; *tent.* tentacles. The ganglion, which is not indicated, lies just below the middle of the stroke from *mo.*

hitherto mentioned can be shown, by using appropriate tests, to be composed of some material akin to chitin in composition. The chitinous wall of the zoœcia is the hardened and thickened cuticle of the zooids, having beneath it the soft body-

wall.[1] The anterior region of the body of the zooid forms an *introvert, i.e.*, is capable of being involuted like the finger of a glove within the more posterior part: the cuticle covering this, continuous behind with the thick ectocyst, is quite thin and flexible. When the introvert is everted it is seen to bear at its anterior end a circlet of usually fourteen long, slender filiform tentacles (*tent.*) on a circular ridge or *lophophore* surrounding the mouth of the zooid. The tentacles are densely ciliated except along their outer surfaces: the cilia vibrate actively in such a way as to drive currents of water, and with them food-particles, towards the mouth (*mo.*): they are also capable of being bent in various directions. In the interior of each is a narrow prolongation of the cœlome. In all probability besides bringing minute particles of food to the mouth of the zooid by the action of their cilia, the tentacles are tactile, and also act as organs of respiration. When retracted they become enclosed by the walls of the introvert as by a sheath—the *tentacle-sheath*. A pair of bands of muscular fibres—the *parieto-vaginal* muscles (*ret.*)—passing to the introvert from the body-wall, serve to retract the introvert and tentacles.

The **body-wall** consists, in addition to the cuticle of an epidermis composed of a single layer of large flattened cells, two muscular layers, the outer circular and the inner longitudinal, and a layer of an irregular cellular tissue, or parenchyma.

The **cœlome** is extensive; it is lined externally by the parietal layer of parenchyma forming the innermost layer of the body-wall, and internally by a visceral layer of the same tissue, ensheathing the alimentary canal. Across the cavity between the parietal and visceral layers of the parenchyma pass numerous strands of spindle-shaped cells. A large double strand (*funic.*) passes from the proximal or aboral end of the alimentary canal to the aboral wall of the zoœcium; this is the *funiculus*. A transverse partition cuts off (though not completely) a small anterior compartment of the cœlome from the rest. The former surrounds the bases of the tentacles, the narrow internal cavities of which are in communication with it: this is known as the *circular canal*. The cœlomic fluid contains a number of colourless corpuscles or leucocytes.

Alimentary Canal.—The mouth (*mo.*) leads into a wide chamber—the *pharynx* (*ph.*)—just behind the bases of the tentacles; from this a somewhat narrower short tube, separated by a constriction from the pharynx, leads to to the *stomach* (*stom.*) from which it is also separated by a constriction. The stomach gives off a long conical prolongation or *cæcum* passing towards the aboral end of the zoœcium, to which it is attached by the funiculus. The *intestine* (*int.*) comes off from the oral aspect of the stomach, not far from the œsophagus, with which it lies nearly parallel: it terminates in a rounded anal aperture (*an.*) capable of being distended to a considerable size, situated not

[1] The terms *ectocyst* and *endocyst* are commonly applied respectively to the hardened cuticle of the zooid and its soft body-wall.

far from the mouth, but outside the lophophore. The entire alimentary canal is lined by an epithelium, which is ciliated throughout except in a portion of the stomach : the cells of the epithelium, which are arranged in a single layer, vary in length in different regions, being longest in the pharynx, which is comparatively thick-walled. A pair of slender muscles (*gast.*) passing from the body wall to the stomach act as *retractors* of the alimentary canal when the introvert is drawn back.

There are no blood-vessels.

The **nervous system** consists of a small round ganglion situated between the mouth and the anus, giving off nerves to the various parts ; sense-organs are absent. Definite **excretory organs** do not occur in Bugula, the function of

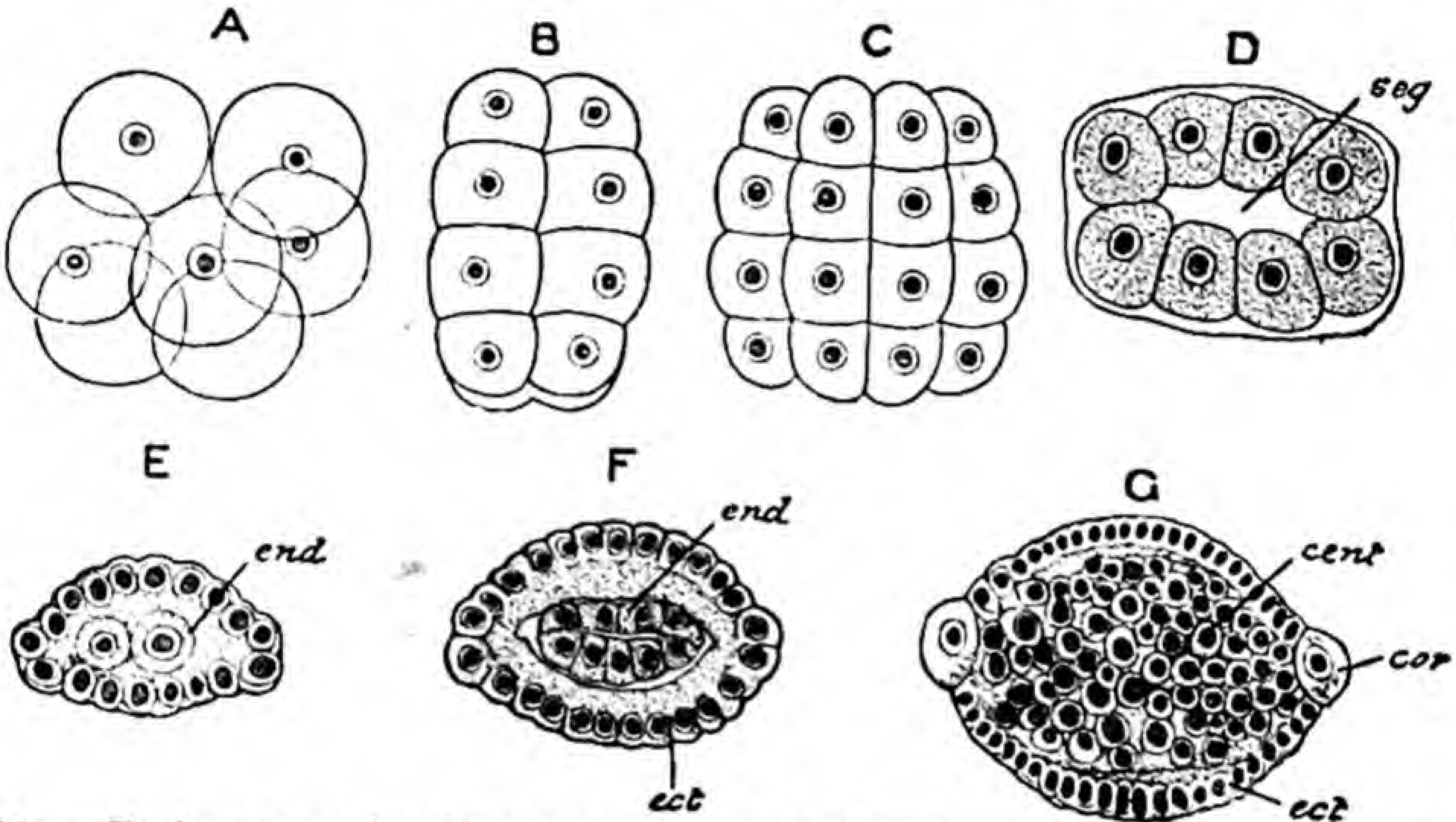


FIG. 661.—Early stages in the development of **Bugula.** *cent.* central mass of cells ; *cor.* corona ; *ect.* ectoderm ; *end.* endoderm ; *seg.* blastocœle. (After Vigelius.)

excretion (*i.e.*, the collection of the nitrogenous waste-matters) being apparently carried on by the leucocytes and the cells of the funicular tissue.

Reproductive Organs.—Ovary and testis are found to occur together in the same zooid. They are both formed from specially modified cells of the parenchyma, either of the funiculus or of the body-wall. The testis, developed from the cells of the funicular tissue, gives origin to spherical masses of cells—the *spermatidia* (*sp.*)—which develop into sperms with very long motile tails. These become free from one another and move about in the body-cavity or in its prolongations into the tentacles. There is no sperm-duct, and it is doubtful if the sperms pass to the exterior. The ovary (*ov.*) is a small rounded body formed from the parietal layer of the parenchyma about the middle of the zoœcium ; it consists of only a small number of cells of which only one at a time becomes a mature ovum, certain smaller cells forming an enclosing follicle. The mature ovum is perhaps fertilized in the cœlome ; it passes into the interior of a rounded outgrowth of the zoœcium—the *oœcium* (*oœc.*)—lined with

parenchyma, and forming a sort of brood-pouch in which it undergoes development.

Development.—Cleavage (Fig. 661) is complete and nearly regular. A blastula is formed having the shape of a bi-convex lens. In the interior of the blastocœle or cavity of the blastula, four cells (*end.*)—the primitive endoderm cells—become distinguishable; these increase in number by division, and form a mass of free cells which almost completely fill the blastocœle; this mass apparently represents both endoderm and mesoderm. Small cavities which appear in it subsequently unite together to form the primitive cœlome. A very broad ring-shaped thickening—the *corona* (*G, cor.*)—is formed round the equator of the embryo and becomes provided with cilia. A circular *pallial groove* arises on the oral side of the corona. A sac-like, afterwards beaker-shaped

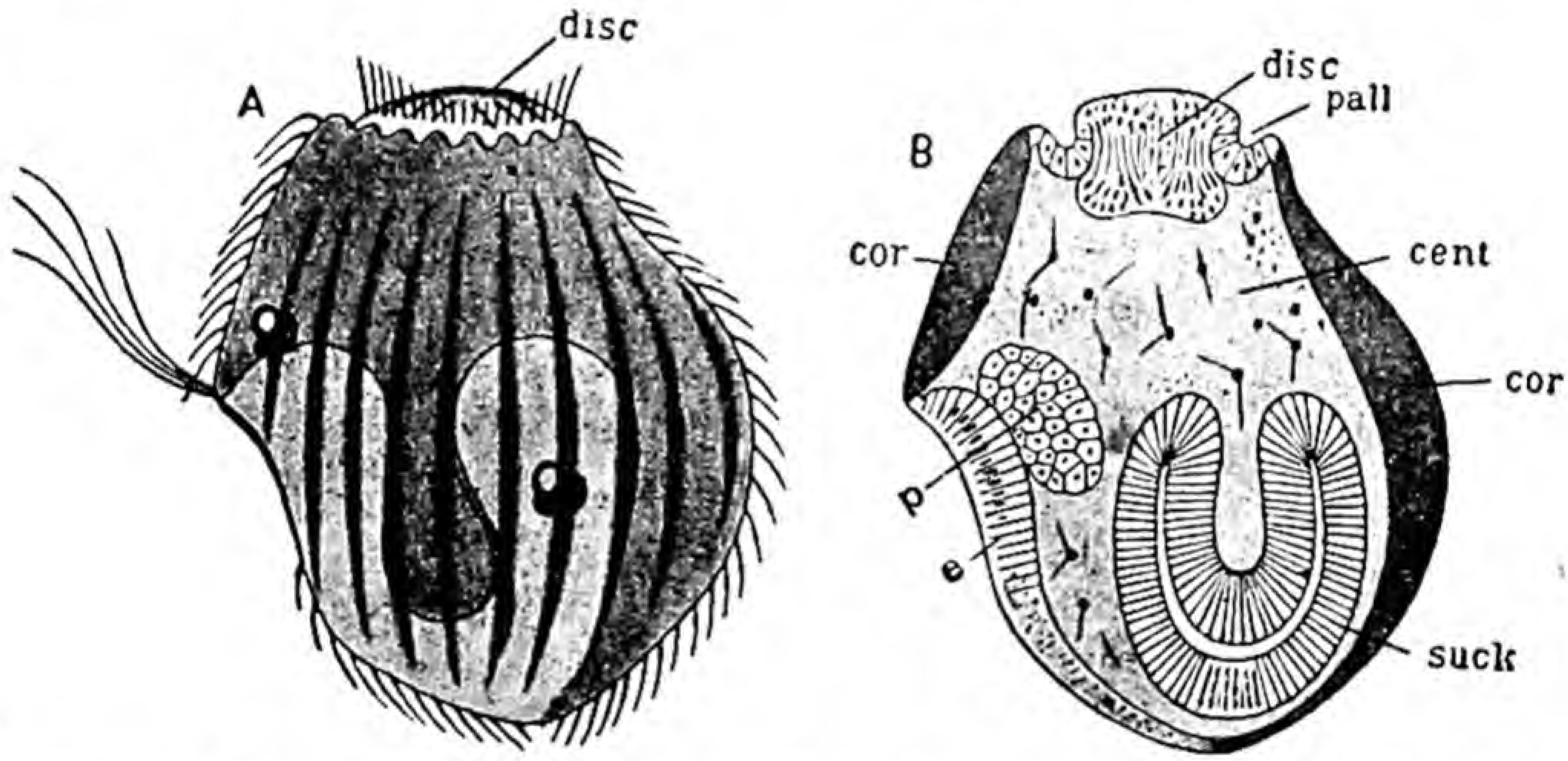


FIG. 662.—*A*, Larva of **Bugula plumosa**; *B*, Sagittal section of larva of **Bugula** (diagrammatic). *cent.* central tissue; *cor.* corona; *disc.* retractile disc; *e.* ectodermal groove; *p.* pyriform organ; *pall.* pallial groove; *suck.* sucker. (From Korschelt and Heider, after Barrois.)

invagination of the ectoderm on what is destined to become the oral side of the ciliated ridge, forms a larval structure, termed the *sucker* (Fig. 662 *suck.*), which afterwards serves to fix the larva. A second depression of the ectoderm in the region of the corona on the oral side forms the *ectodermal groove.* At the aboral pole is developed, also from the ectoderm, a second larval structure—the *calotte* or *retractile disc* (*disc*), on which motionless sensory cilia appear. In close relation to the ectodermal groove is formed a mass of cells, the *pyriform organ* (*p.*) which seems to have a sensory function.

An alimentary canal is absent in the larva of Bugula when it escapes from the oœcium. After an interval of free existence as a ciliated larva, certain changes appear which lead to a very complete metamorphosis. The sucker becomes everted by a strong contraction of the body, and fixes the larva to some foreign object. The aboral side of the larva becomes greatly extended,

so that almost the entire integument of the primary zooid is developed from this part (*i.e.*, from the region occupied by the retractile disc and pallial groove). Accompanying the extension of the aboral surface are the obliteration of the pallial groove and the bending down of the corona towards the oral side. Thus the stage of the larva termed the *umbrella-shaped* stage is reached. The sucker is everted, and by means of it the larva becomes attached. The edge of the "umbrella" becomes bent downwards, and fused with the broad plate into which the sucker has expanded, thus enclosing a circular cavity, the co-called *vestibule* (Fig. 663, *v.*). The walls of this, consisting of the coronal cells and a portion of the original sucker, become broken up and the cavity is merged in the general cavity in the interior of the larva. All the larval structures have now disappeared with the exception of the basal plate of the sucker and the retractile disc. The former gives rise to the basal part of the wall of the primary zoœcium. From the latter, which becomes invaginated, or from a sac which is developed to replace it, are developed both the ectodermal and endodermal structures of the primary zooid. Occupying the interior of the larva at this stage in addition to this sac, there is only a mass of undifferentiated tissue derived from the original central tissue together with that derived from the disintegrated corona, pyriform organ, and part of the sucker. The outer wall forms the wall of the primary zoœcium, the surface of which becomes covered with a chitinous cuticle or ectocyst. Most of the internal mass goes to form a *brown body*, which now becomes developed, but a part of it seems to form the mesoderm of the zooid. A diverticulum of the sac constitutes the first rudiment of stomach and intestine; a second diverticulum forms the rudiment of the œsophagus; these become applied to one another and fuse to form the continuous alimentary canal. The ganglion arises as an invagination of the ectoderm in the space between mouth and anus. The upper part of the cavity of the primitive sac, after the rudiment of the alimentary canal has been separated off, forms a space termed the *atrium*; the walls of this become converted into the tentacle sheath, while on its base appear the rudiments of the tentacles and lophophore. During the development of the organs of the adult zooid the brown body becomes closely applied to the stomach and gradually absorbed.

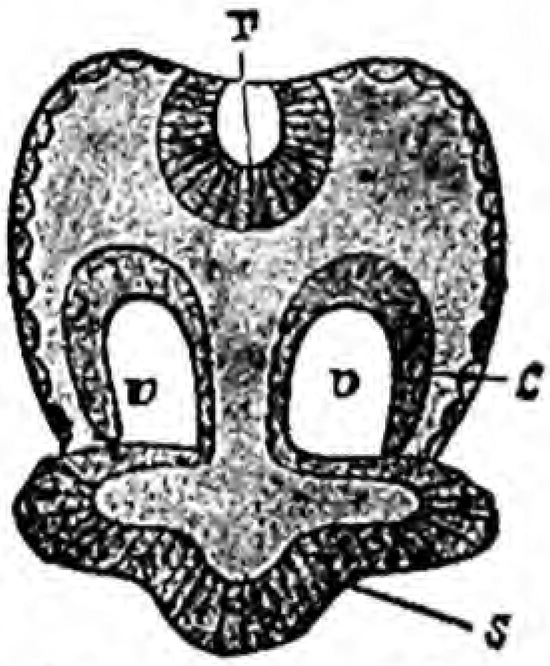


FIG. 663. — Longitudinal section of attached larva of **Bugula.** *c.* cells of corona; *r.* rudiment of the zooid in the form of a sac; *s.* basal plate of everted sucker; *v.* vestibule. (From Korschelt and Heider, after Barrois.)

The primary zooid thus formed gives rise asexually by a process of repeated budding to the branching structure which has been described. In many of the zoœcia of a fully-developed colony no zooid is found to be present, but, instead, there is a dark brown body similar to that which occurs in the primary zoœcium. This is a zooid that has undergone degeneration—the lophophore tentacles,

and alimentary canal having been absorbed. Such degenerated zooids are capable of regeneration, the organs becoming re-developed and the brown body re-absorbed.

2. Distinctive Characters and Classification.

The Bryozoa form colonies of zooids connected together by a common organic substance. There is a lophophore bearing a series of slender, ciliated, post-oral tentacles. The anterior part of the body forms a short introvert, within which the lophophore and the tentacles are capable of being withdrawn. In some the prostomium is represented by a small lobe—the epistome. The alimentary canal is U*-shaped, and the anus is anterior, just outside the tentacular circlet. In most the nervous system is represented only by a small ganglion between the mouth and the anus. A cuticle, sometimes gelatinous, sometimes horny, sometimes calcified, forms a firm exoskeletal layer for the support of the colony. Excretory organs are absent. There is no vascular system. The sexes are usually united. The majority of Bryozoa occur in the sea; a limited number are inhabitants of fresh-water.*

Order 1.—Phylactolæmata.

Fresh-water Bryozoa with horse-shoe-shaped lophophore and with an epistome.

Including *Cristatella* (Fig. 665), *Plumatella* (Fig. 664), *Fredericella*.

Order 2.—Gymnolæmata.

Almost exclusively marine Bryozoa, with a circular lophophore, and without an epistome.

Sub-order a.—Cyclostomata.

Gymnolæmata with tubular calcareous zoœcia having circular apertures devoid of closing apparatus.

Including *Crisia*, *Idmonea*, etc.

Sub-order b.—Cryptostomata.

Palæozoic Gymnolæmata resembling Cyclostomata, but with the aperture lying at the bottom of a funnel-shaped shaft—the vestibule. The tubes are partitioned by diaphragms.

Including *Fenestella*, *Rhabdomeson*, etc.

Sub-order c.—Trepostomata.

Mainly palæozoic Gymnolæmata, generally with massive zoaria of parallel, tubular, clacareous zoœcia, like those of Cyclostomata, but crossed by numerous diaphragms; the lower "immature" portions of the tubes are thin-walled and of one kind, while the upper, "mature" portions are thick-walled, and di- or poly-morphic.

Including *Monticulipora*, *Heterotrypa*, *Stenopora*, etc.

Sub-order d.—Cheilostomata.

Gymnolæmata with calcareous or chitinous zoœcia usually provided with opercula.

Including *Bugula* (Fig. 660), *Flustra* ("Sea-mat"), *Membranipora*, *Cellepora*, *Selenaria*.

Sub-order e.—Ctenostomata.

Gymnolæmata with chitinous or gelatinous zoœcia provided with a series of tooth-like processes closing the aperture when the tentacles are retracted.

Including *Alcyonidium*, *Serialaria*, *Paludicella*.

3. General Organization.

The Bryozoa are all colonial—the colonies being capable, in most cases, like the colonies of hydroid Cœlenterates, of increasing in size to an apparently in-

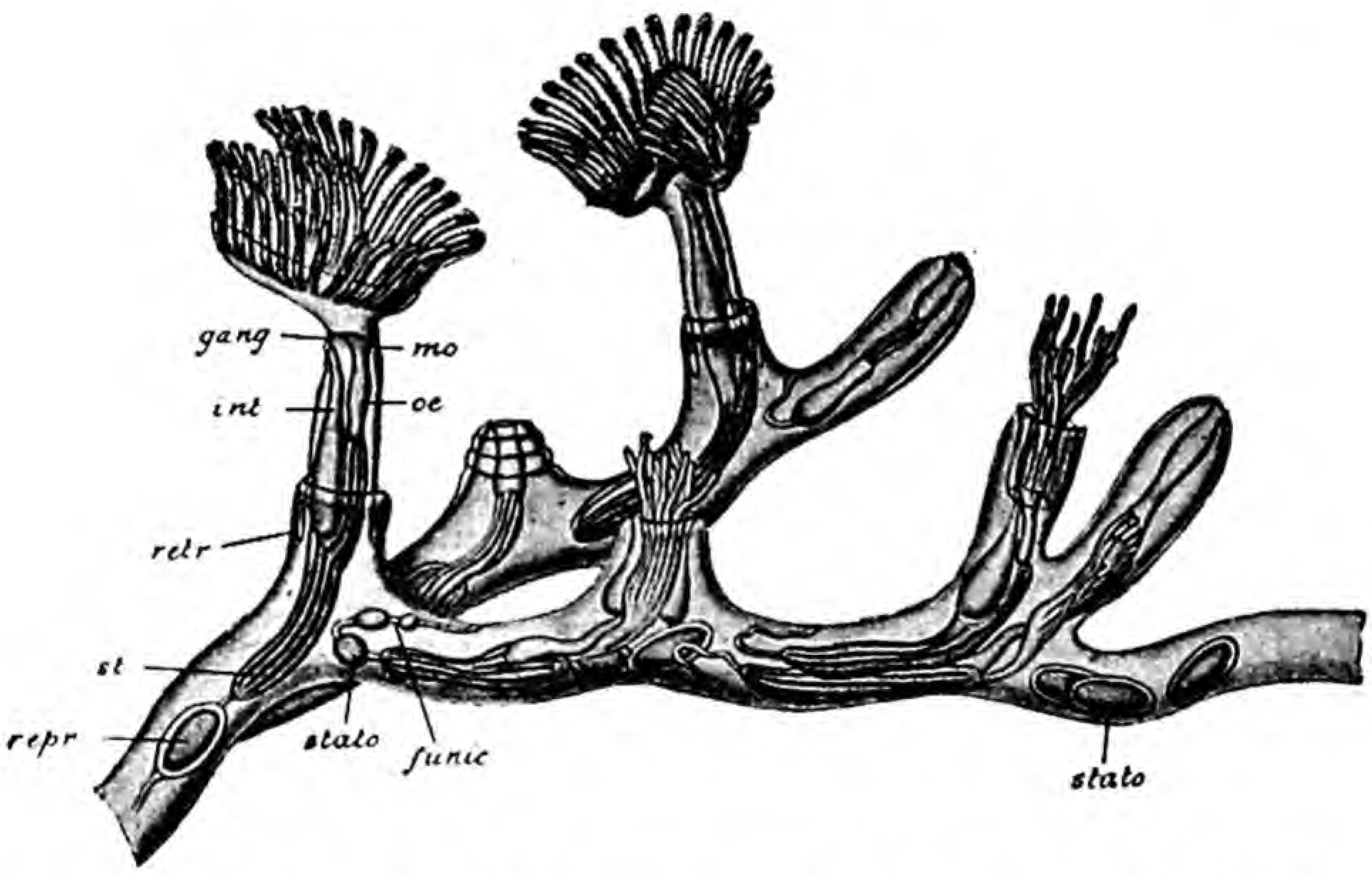


Fig. 664.—**Plumatella.** Portion of a colony, magnified. *funic.* funiculus; *gang.* ganglion; *int.* intestine; *mo.* mouth; *œ.* œsophagus; *repr.* gonad; *retr.* retractor muscle; *st.* stomach; *stato.* statoblasts. (After Allman.)

definite extent by continuous budding. The thickened cuticle which forms the support of the colony is sometimes gelatinous, sometimes chitinous, sometimes chitinous with sand-grains affixed, sometimes calcareous. The form of the colony varies in different families and genera in accordance with differences in the shape of the constituent zoœcia, and differences in their mode of budding and consequent arrangement. The zoœcia are sometimes tubular, sometimes ovoid, sometimes, polyhedral. In some cases the buds are so developed that

the colony assumes the form of a thin, flat expansion, which may be encrusting, and consist of a single layer of zoœcia in close contact with one another or connected together by tubular processes; or may be erect, and with the zoœcia either in one or two layers: sometimes the lamellar colony thus formed may be fenestrated or divided into lobes; sometimes it is twisted into a spiral. In other cases the colony, instead of being lamellar, has the form of an erect shrub-like structure, consisting of numerous cylindrical, many-sided, or strap-shaped branches arising from a common root. Sometimes there is a creeping cylindrical

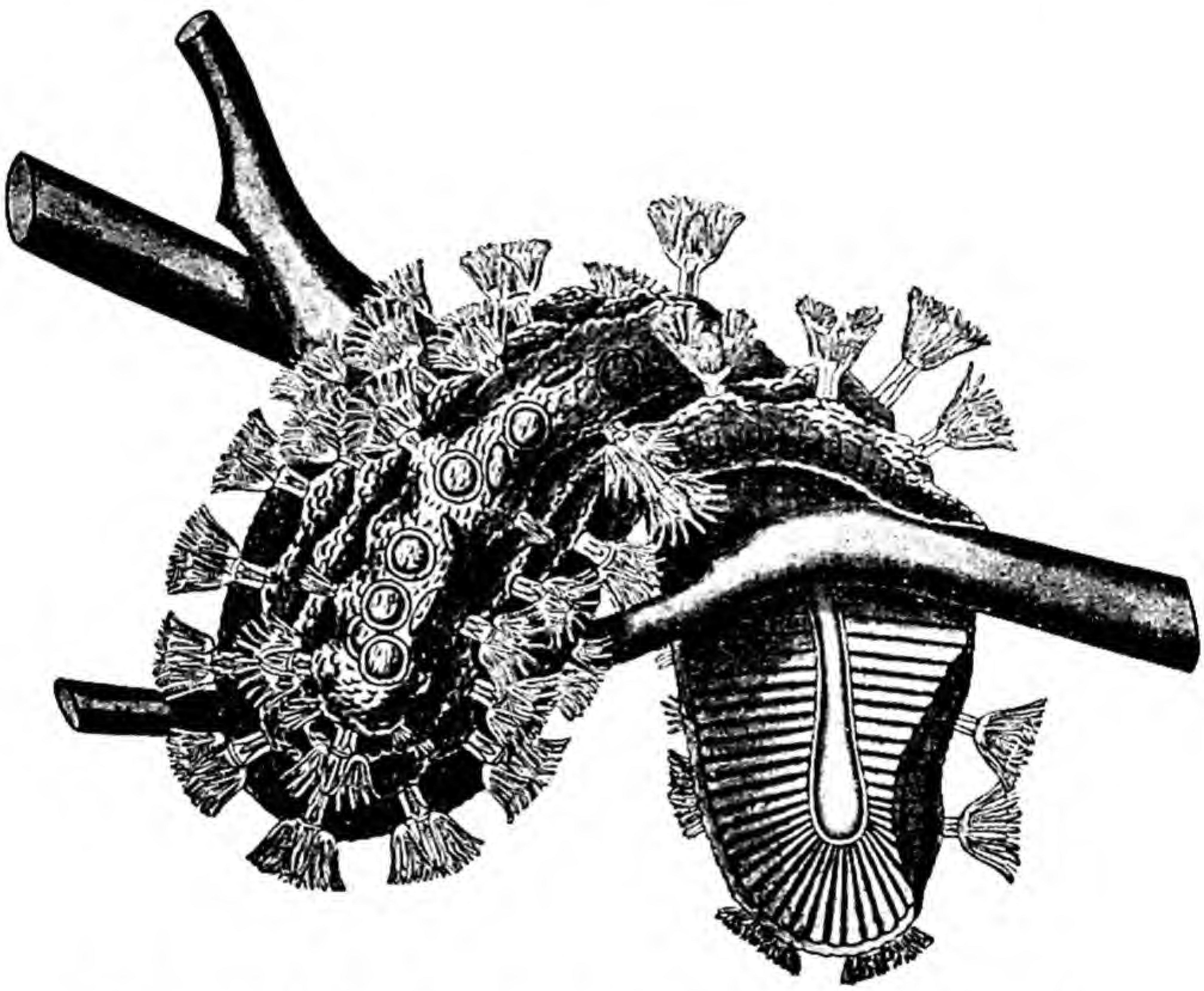


FIG. 665.—**Cristatella mucedo.** Entire colony. (After Allman.)

stolon, simple or branched, having the zooids arranged along it in a single or double row. The colony is free only in *Cristatella* (Fig. 665)—in which it performs creeping movements, in some other (American) forms of Phylactolæmata (in the younger stages of the colony), in one family of the Cheilostomata—the *Selenariidæ* (in which it moves along with the aid of certain peculiar appendages —the *vibracula*—to be described subsequently), and in one or two other cases.

The zoœcia open on the exterior by means of circular, semi-circular, or crescentic apertures, which in the Phylactolæmata and the Cyclostomata among the Gymnolæmata are devoid of any special closing apparatus; while in the Cheilostomata there is a movable lid or *operculum* closed by a pair of *occlusor*

muscles when the introvert is retracted; and in the *Ctenostomata* there is a series of lobes or teeth which close in together over the opening. The cavities of the neighbouring zoœcia are in some forms completely cut off from one another by a continuation of the chitinous or calcareous exoskeleton; in others there is free communication; in others, again, there is communication through a number of minute perforations.

The oral (anterior) part of the body of each zooid is, as already described in the case of Bugula, covered only with a thin and flexible cuticle, and forms an *introvert* capable of being retracted into the interior of the zoœcium. At the free end of the introvert is the mouth surrounded by a lophophore bearing tentacles. The tentacles are always simple, filiform, and hollow, each containing a narrow diverticulum of the *circular canal* or anterior compartment of the cœlome. They are beset with vibratile cilia by means of which currents are created subserving alimentation and respiration. They are also highly sensitive, and are capable of being bent about in various directions by the contraction of muscular fibres in their walls. In the Phylactolæmata (Fig. 664) the lophophore is horse-shoe-shaped, in the Gymnolæmata (Fig. 660) circular: in the former, but not in the latter, there is a ciliated lobe, the *epistome* (Fig. 666, *ep.*)—which may have a sensory function—overhanging the mouth on the anal side. The retraction of the introvert is effected by a pair of bands of muscular fibres, the *parieto-vaginal* muscles, passing to it from the body-wall, and by a pair of retractor muscles passing from the latter to the alimentary canal.

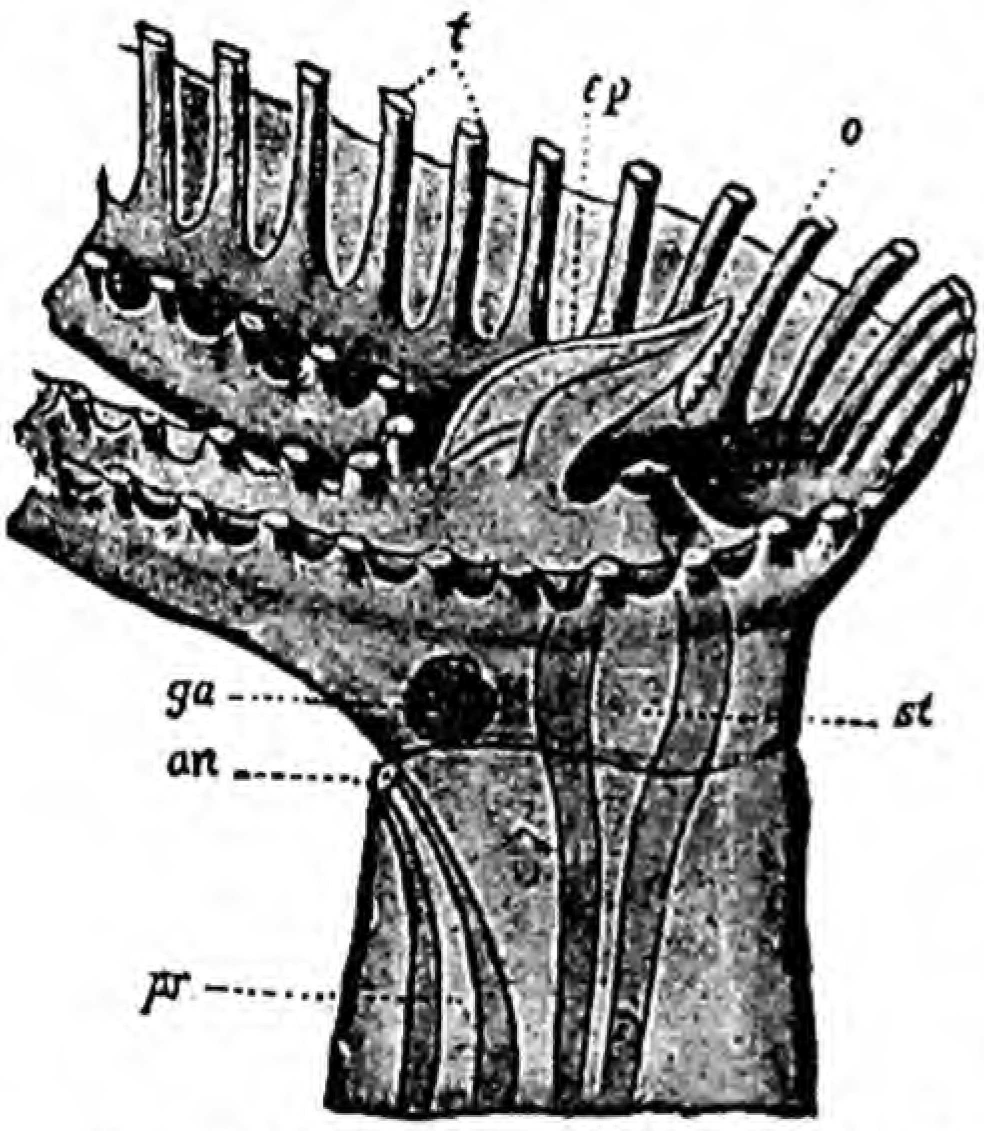


FIG. 666.—Anterior portion of the body of **Lophopus,** from the right side. *an.* anus; *ep.* epistome; *ga.* ganglion; *o.* mouth; *pr.* intestine; *st.* œsophagus; *t.* tentacles, cut off near the base. (From Lang's *Comparative Anatomy,* after Allman.)

Structure of Body-wall.—Beneath the cuticle is an epidermis, consisting of a single layer of flattened polygonal cells, firmly united together by their edges. Beneath this there is usually, but not always, a layer of muscle, which is arranged in two strata—an external composed of circular, and an internal of longitudinal fibres. There is an extensive cœlome lined in some forms (Phylactolæmata) by a definite cœlomic epithelium, in part ciliated; while in others there is no such definite epithelium, but its place is taken by thin parietal and visceral layers of an irregular cellular tissue—the *parenchyma*. Crossing the cœlome are strands, in some instances very numerous, of spindle-shaped cells. In some cases two mesenteric bands suspend the alimentary canal—an anterior attached near the mouth and a posterior passing from the cæcum to the aboral

end of the zoœcium; in most cases the latter, to which the special name of *funiculus* is given, is alone present.

The **alimentary canal** has in all species the parts that have been already described in the case of Bugula. In some of the Cheilostomata it is stated that the cells of the œsophagus bear numerous striated muscle-fibre processes. In some Ctenostomata there is in addition a thick-walled chamber—the *gizzard*—with chitinous teeth, between the œsophagus and stomach.

The **nervous system** consists of a single, sometimes bilobed, ganglion (Fig. 664, *gang.*, and Fig. 666, *ga.*) placed between the mouth and the anal aperture, and of the nerves passing from it to the various parts. There are never any sense-organs, unless the epistome of the Phylactolæmata be of that nature.

Excretory structures are not known with certainty to exist in any of the Bryozoa. In some there is a pore through which water enters the body-cavity, or a ciliated *intertentacular tube* opening at the base of the tentacles. Excretion appears to be performed by certain cells of the funicular tissue and of the parenchyma or cœlomic epithelium. These become loaded with the products of excretion, and are set free as leucocytes in the cœlome, whence they may pass out through the intertentacular tube or may accumulate in the cells of the *brown body*.

In many Bryozoa the colony bears a series of remarkable appendages—the **avicularia**—which are of the nature of modified zooids. In typical cases the avicularium has the bird's-head-like form that has been already described in the case of Bugula; sometimes it is completely sessile. A second set of movable appendages found in some forms are the **vibracula**; these are long tapering whip-like appendages which execute to-and-fro movements. Intermediate forms between avicularia and vibracula show that the latter are extreme modifications of the former. The avicularia are frequently found to have seized in their jaws minute Worms or Crustaceans, and it is probable that their function as well as that of the vibracula, is defensive; in the case of the *Selenariidæ*, which form unattached colonies, it is said that the movements of the vibracula subserve locomotion.

The fertilized ova in many cases undergo the early stages of their development in certain dilatations of the colony (Fig. 660, *oœc.*), and in many of the Gymnolæmata (Cheilostomata) these *ovicells* or *oœcia*, as they are termed, take on a very definite shape.

Reproduction and Development.—In general the Bryozoa are hermaphrodite. Both ovary and testis are derived from the layer lining the cœlome (parenchyma or cœlomic epithelium as the case may be), or from the funicular tissue. The testis may be single or double. The spermatidia, as in Bugula, or the mature sperms, become free in the cœlome. The ovary is very generally situated towards the oral end or about the middle, the testis towards the base. The mature ova escape into the cœlome, and there, in some forms, become fertil-

ized apparently by the spermatozoa of the same individual. The development of the larva may take place in the cœlome or in a special diverticulum of it; in the Cheilostomata the fertilized ova pass into the ovicells (oœcia); in some cases, both among the Phylactolæmata and the Gymnolæmata, they are received into a sheath formed by the tentacles of an imperfectly-developed zooid formed in a zoœcium in which the original zooid had undergone degeneration.

In those cases in which the early stages of development are passed through in the body-cavity of the parent, the ciliated embryos may either escape through the zoœcial aperture after the zooid has undergone degeneration, or through a special opening formed for them in the wall of the zoœcium. In some the fertilized ova pass out through the intertentacular tube, which plays the part of an oviduct. In *Crisia* and other Cyclostomata each of the ripe oœcia is found to contain a large number of embryos, developed from one ovum. The ovum in this genus cleaves to form a mass of cells from which finger-like processes arise, the end of each of these becoming constricted off to form an embryo.

Cleavage is total and approximately equal. The form of the free-swimming larva varies considerably, but in most there is a circular band with very long cilia, the *corona*, which may represent the tentacular crown of the adult; this divides the surface into two regions—oral and aboral. The larva may or may not be provided with a digestive canal. The aboral portion of the body presents a ciliated *retractile disc* or *calotte*, which subsequently becomes a closed sac destined to give origin to the primary zooid of the colony; on the oral side is the *sucker* by which the larva afterwards becomes fixed. By a metamorphosis similar to that which has been described in the case of *Bugula* a primary zoœcium with a primary zooid is developed from the previously free ciliated larva. In *Membranipora*, which belongs to the Cheilostomata, and in several genera of Ctenostomata, the larva (called *Cyphonautes* when it was supposed to be an adult animal) is laterally compressed, with a bivalve shell. In the Cyclostomata the larva is barrel-shaped, with the mouth at one end, and at the other a prominence corresponding to the retractile disc. In the Phylactolæmata the larva is in the form of a ciliated hollow cyst from which the colony is formed by gemmation. A special form of asexual multiplication by means of bodies termed *statoblasts* (Fig. 664, *stato.*) is observable in the Phylactolæmata. The statoblasts are internal buds formed from the funiculus and enclosed in a chitinous shell; they are set free eventually by the death and decay of the parent colony, and each gives rise to a small zooid which fixes itself and develops into a colony.

Mode of Life and Distribution.—None of the Bryozoa are parasites in the strict sense of the term, but very many of them live in intimate association with other organisms, often growing over and through them so as to form with them

one complex structure. Certain genera are able by some means to excavate minute burrows in the shells of bivalves.

The majority of Bryozoa are marine; but all the Phylactolæmata, together with Paludicella of the Ctenostomata, are inhabitants of fresh water. The fresh-water forms inhabit both running and stagnant waters; they occur at all elevations and are represented in all the great regions of the earth's surface. The marine forms are most abundant at moderate depths; but representatives of the group have been dredged from as great a depth as over 3,000 fathoms. In certain localities the larger kinds grow in great luxuriance, so as to form miniature forests.

Geologically the Bryozoa are a very ancient group, being represented in the Cambrian and later Palæozoic formations by Cyclostomata, Cryptostomata and Trepostomata. In the later formation of the Mesozoic period the Cheilostomata are also abundantly represented, and in the Tertiary the latter sub-order greatly outnumbers the Cyclostomata. The Tertiary Bryozoa flourished in certain localities in such luxuriance that their remains form calcareous deposits of very great extent.

THE PHORONIDA.

The position of Phoronis and its close ally Phoronopsis, worm-like marine animals, is a matter on which widely divergent views are held. On account of certain resemblances to the Bryozoa, and, more particularly, to the Phylactolæmata they are often looked upon as related to that class and to the Brachiopoda (*vide infra*).

Phoronis (Fig. 667) lives in associations consisting of a number of individuals. These are usually looked upon as having all been developed from ova. Each worm is enclosed in a membranous or leathery tube, within which it is capable of being completely retracted. The body, which varies in length in the different species from 1·5 to 127 mm., is cylindrical, elongated, and unsegmented. At one end there is a crown of numerous slender, ciliated tentacles borne on a horse-shoe-shaped lophophore, the lateral cornua of which are spirally coiled in the larger species; these are supported by a mesodermal skeleton and are non-retractile.

Both mouth and anus (Fig. 668, *mo.*, *an.*) are situated at this tentacular extremity of the body, separated from one another by only a short space. This

short space between mouth and anus represents, as in the Bryozoa, the greatly abbreviated *dorsal surface*; but it will be convenient to term this end of the animal the anterior, and the opposite the posterior end: the side of the elongated body towards which the mouth is approximated may be distinguished as the *oral*, the opposite as the *anal*. A broad lobe—the *epistome* (*ep.*)—overhangs the mouth and lies between it and the anus. Near the anus open two ciliated *nephridial tubes* (*nephr.*), which open internally each by two apertures into the posterior chamber of the cœlome.

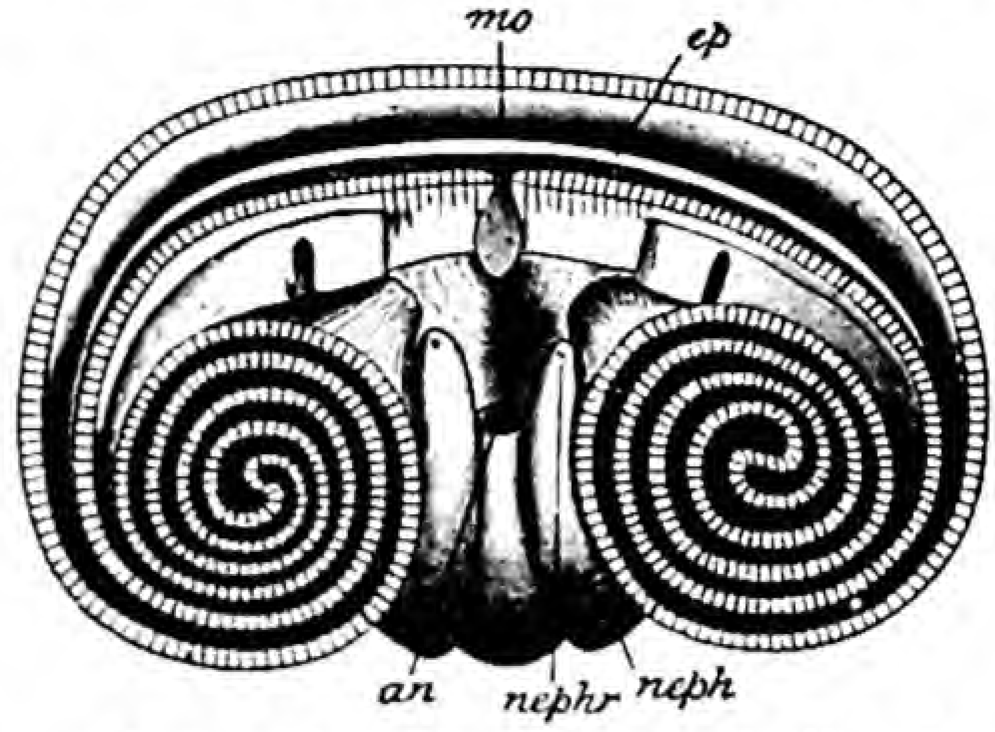


FIG. 668.—**Phoronis australis**, free end, magnified. *an.* anus; *ep.* epistome; *mo.* mouth; *nephr.* nephridial aperture; *neph.* nephridium. (After Benham.)

FIG. 667.—**Phoronis australis**, natural size.

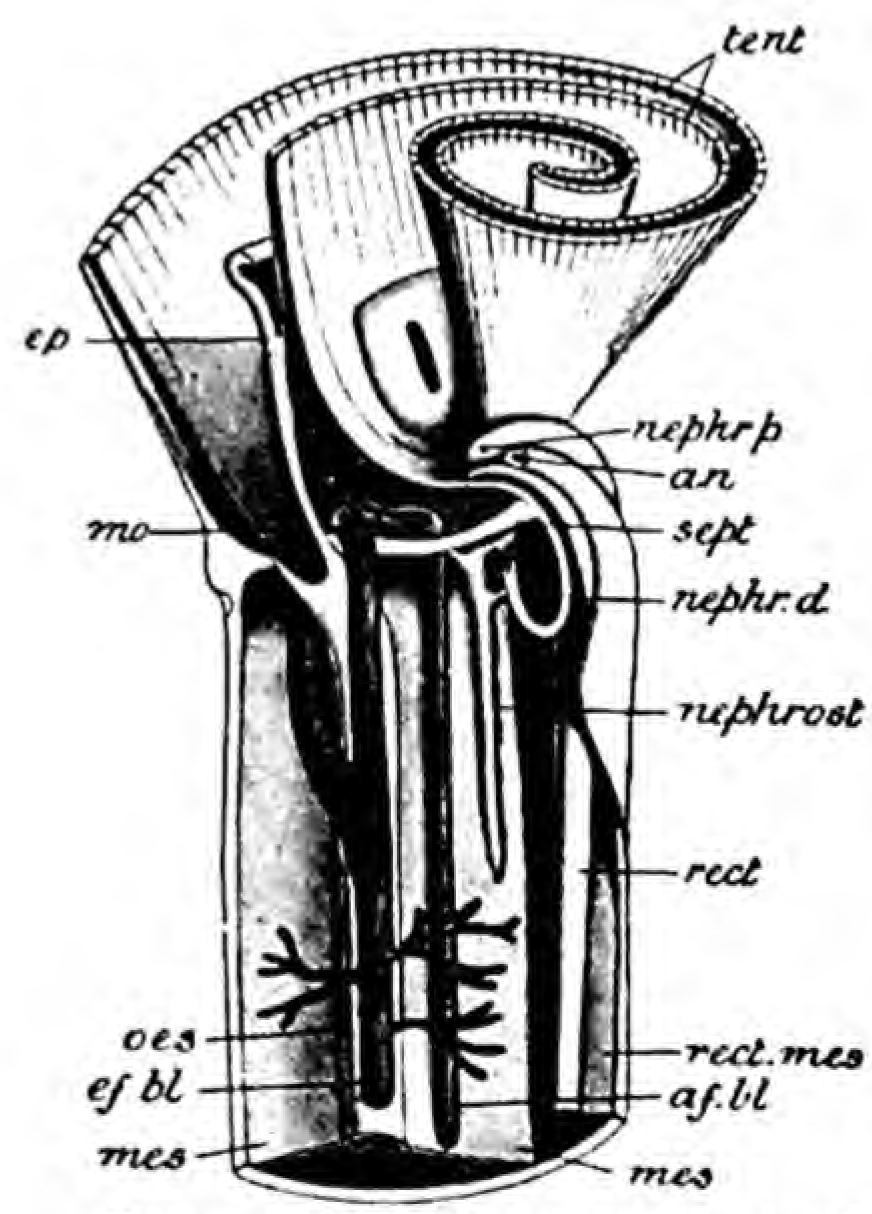


FIG. 669.—**Phoronis australis**, internal organization. *af. bl.* afferent blood vessel; *an.* anus; *ef. bl.* efferent blood-vessel; *ep.* epistome; *mes.* mesentery; *mo.* mouth; *nephr. p.* nephridiopore; *nephr. d.* duct of nephridium; *nephrost.* nephrostome (internal opening of nephridium); *œs.* œsophagus; *rect.* rectum; *rect. mes.* rectal mesentery; *sept.* septum; *tent.* tentacles (cut short). (After Benham.)

The *cœlome*, which is lined with a cœlomic epithelium, is divided into two parts of very unequal extent by a partition or mesentery which runs across just

behind the tentacles. The anterior part is in communication with cavities in the tentacles and the epistome. The posterior, and by far the most extensive part of the cœlome, occupies the whole of the length of the body behind the transverse partition. It is subdivided into two by a median longitudinal mesentery (Fig. 670, *m.*, *m.*), which extends from the oral to the anal surface and supports both limbs of the alimentary canal; and each of these is further subdivided by a longitudinal mesentery extending from the body-wall to the œsophagus (*œ.*) in the one compartment (usually termed the right), and to the

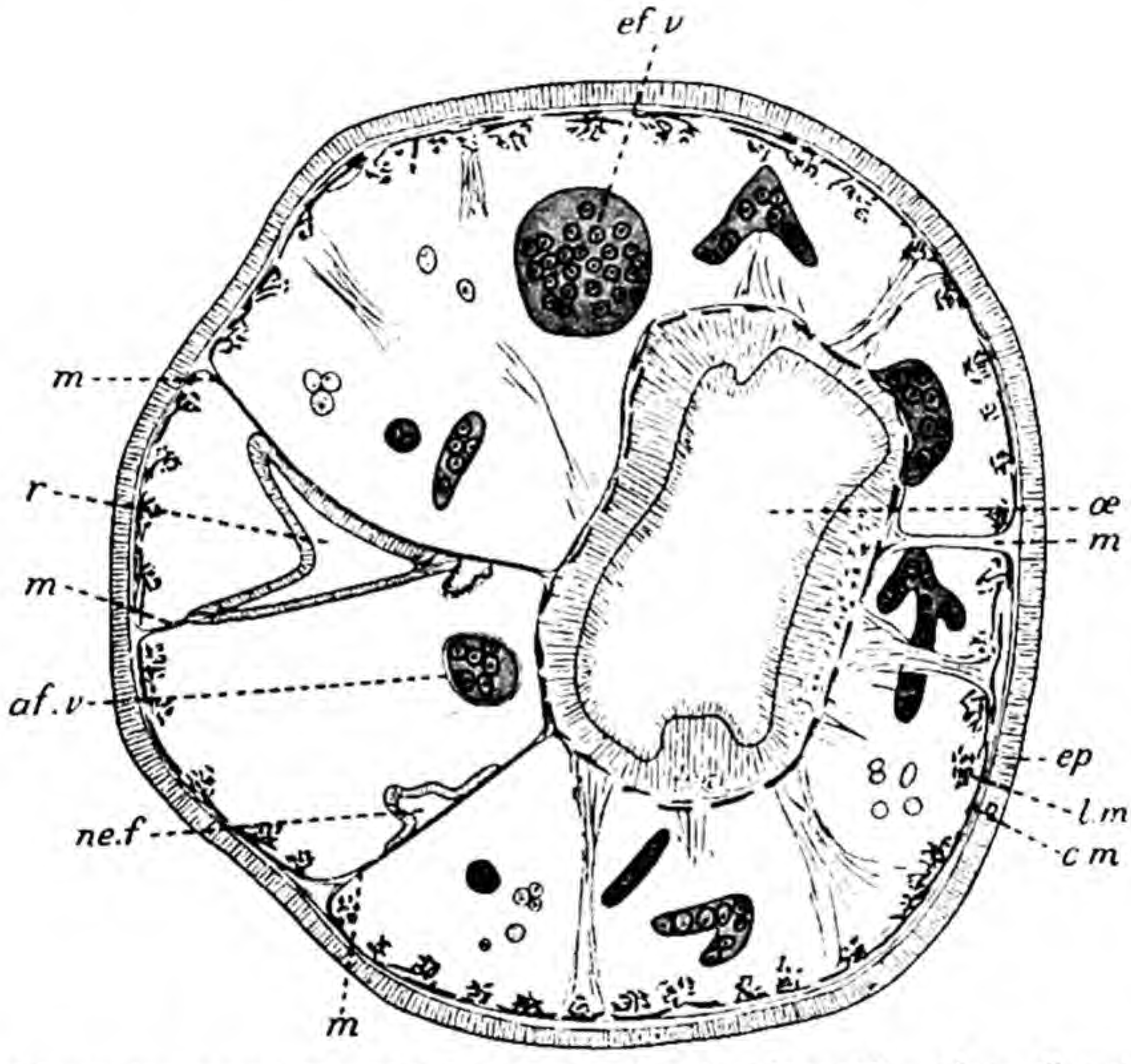


FIG. 670.—**Phoronis,** transverse section towards the anterior end. *af. v.* afferent blood-vessel; *c. m.* circular layer of muscular fibres; *ef. v.* efferent blood-vessel; *ep.* epidermis; *c. m.* circular layer of muscle; *m.*, *m.* mesenteries; *ne. f.* funnel-like opening of nephridium; *œ.* œsophagus; *r.* rectum. (After Benham.)

rectum (*r.*) in the other (left). The *alimentary canal* is bent on itself to form a loop, as in the Bryozoa: it is distinguishable into œsophageal, gastric and intestinal regions. There is a closed system of *blood-vessels* with contractile walls containing red blood-corpuscles. The *nervous system* lies immediately below the cells of the epidermis. Nerve-elements are generally distributed over the surface, but are specially concentrated in the form of a ring surrounding the body just behind the mouth, but not enclosing the anus, thickened into a ganglion between mouth and anus, and giving off nerves to the tentacles. There are no sense-organs.

Phoronis is hermaphrodite. Ova and sperms are developed in the cœlome towards the posterior end from cells on the wall of one of the large blood-vessels. When mature these pass out through the nephridia to the spaces enclosed by the tentacles, where the ova are fertilized (—according to another account, fertilization takes place in the cœlome—), and they go through the early stages of development fixed to the tentacles. The cleavage is complete and slightly unequal : when four blastomeres are formed two larger, darker endoderm and two smaller, clearer ectoderm cells are to be distinguished. A blastula is formed with clearer ectoderm cells on one side ; invagination takes place ; and, as the embryo elongates, the blastopore is drawn out into a slit which eventually becomes closed up behind, the anterior portion alone remaining open to form the mouth. The anus is developed later as an invagination in the position of the posterior part of the former blastopore. The mesoderm is budded off from the endoderm, and the cœlomic spaces are believed to arise as diverticula folded off from the archenteron. A large pre-oral lobe is formed, and the anus becomes surrounded by a circlet of cilia (Fig. 671, *t. tr.*). The part of the body on which the anus is situated becomes elevated into a conspicuous process. Behind the mouth there is a circlet of cilia, and from this region grow out a circlet of processes—the rudiments of the larval tentacles (Fig. 672, *B*). The larva has now reached the stage to which the term *actinotrocha* is applied. It has a large hood-like lobe overhanging the mouth and a circlet of ciliated larval tentacles ; the anus is situated on a prominent process.

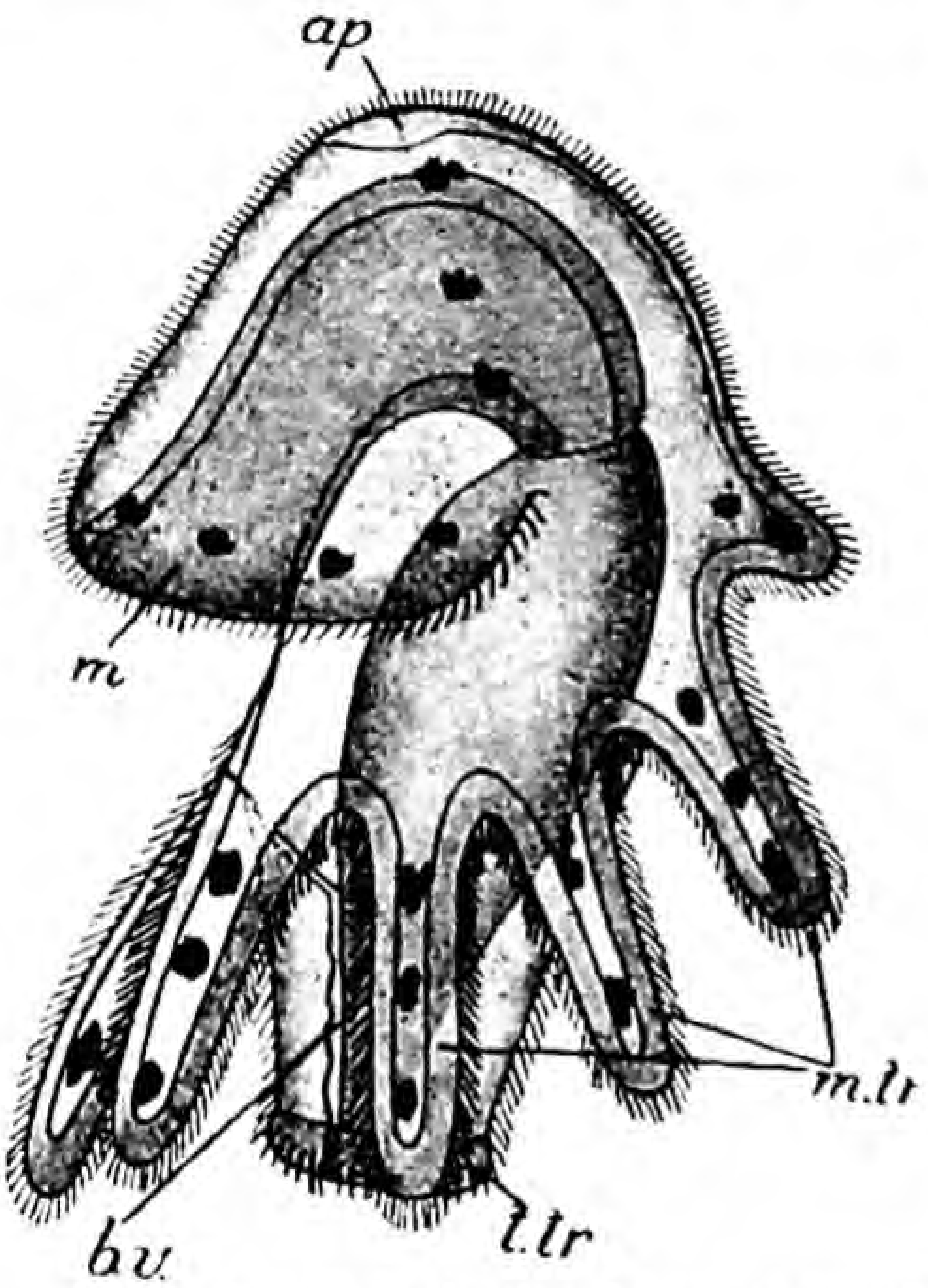


FIG. 671.—**Actinotrocha** larva of **Phoronis,** lateral view. *ap.* apical plate ; *b. v.* blood-vessel ; *m.* mouth ; *m. tr.* circlet of cilia and tentacles ; *t. tr.* circlet of cilia round anus. (From MacBride, after Metschnikoff.)

There is a pair of excretory organs corresponding to those of the trochophore larva ; these have no cœlomic apertures, but are provided with *solenocytes* (see Section VII, Annelida). They are said to become converted into the nephridia of the adult. A thickening of the ectoderm of the pre-oral lobe, sometimes bearing eyespots, appears to represent the apical plate of the trochophore. At the point where the œsophagus opens into it, the gastric region of the alimentary canal gives off forwards in one species a pair of hollow diverticula, the cells of which contain vacuoles like those of the neighbouring parts of the stomach itself (Fig. 294, *C. gl.*).

The ectoderm of the process on which the anus is situated subsequently

becomes involuted to form a deep pit (Fig. 672 A), and rudiments of the adult tentacles (*B*, *a. ten.*) are formed as a ring of processes at the base of the larval tentacles. The metamorphosis from this point is completed with great rapidity. The larva sinks to the bottom; the pit at the side of the anal elevation becomes everted (*B*, *inv.*) and the alimentary canal of the larva is

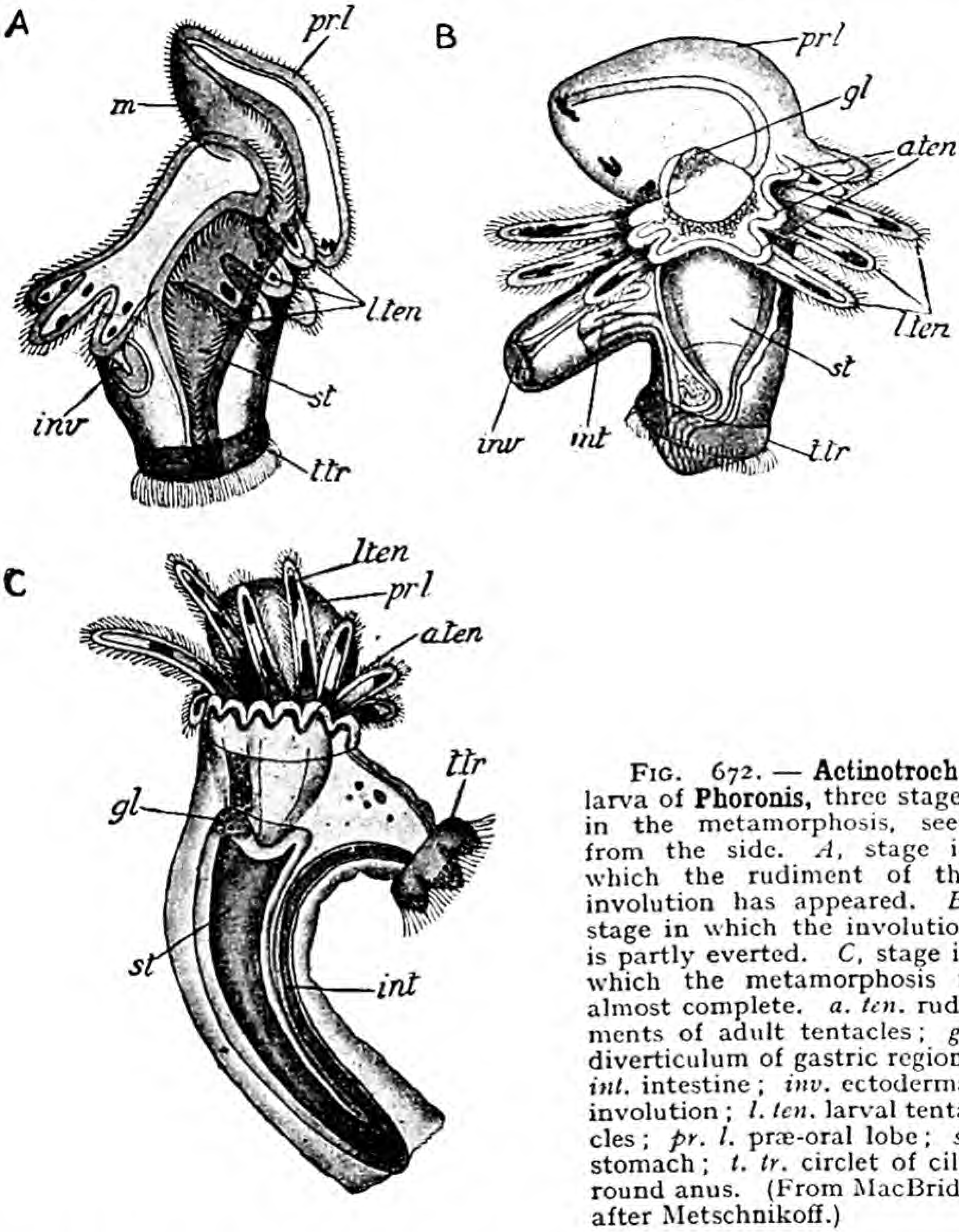


FIG. 672. — **Actinotrocha** larva of **Phoronis,** three stages in the metamorphosis, seen from the side. *A*, stage in which the rudiment of the involution has appeared. *B*, stage in which the involution is partly everted. *C*, stage in which the metamorphosis is almost complete. *a. ten.* rudiments of adult tentacles; *gl.* diverticulum of gastric region; *int.* intestine; *inv.* ectodermal involution; *l. ten.* larval tentacles; *pr. l.* præ-oral lobe; *st.* stomach; *t. tr.* circlet of cilia round anus. (From MacBride, after Metschnikoff.)

drawn into it (*C*), the projection thus formed, which grows out at right angles with the long axis of the larva, becoming the body of the future animal; the larval tentacles and pre-oral lobe are thrown off, and the lophophore is developed.

The Phoronida have a wide geographical distribution, occurring in all the chief regions. Some of the species live about low-water mark: others at

moderate depths up to about thirty fathoms. Some of the associations take the form of encrustations of the matted tubes. In other cases the tubes lie in excavations in stone or in the shells of Molluscs. In one species the tubes occupy channels in the substance of the tube of a Sea-anemone.

THE BRACHIOPODA.

The Brachiopoda are the fabricators of the well-known "Lamp-shells" found in most parts of the world. They occur in the sea at various depths, and were once erroneously classed under the Mollusca, their characteristic bivalved shell being compared with that of Oysters, Mussels, etc.

1. Example of the Class—*Magellania (Waldheimia) lenticularis or M. flavescens.*

Magellania lenticularis is found in great numbers, at moderate depths, off the coast of New Zealand. An allied species, *M. flavescens*, is equally common in the Australian seas, and several other species are known in various parts of the world.

The body is entirely covered by a **shell** (Fig. 673) of oval form and pink colour, composed of two pieces or *valves*, one of which, distinguished as the *ventral valve* (*v. v.*), projects beyond the other or *dorsal valve* (*d. v.*), in the form of a short conical *beak* (*b.*) perforated at the end by an aperture, the *foramen* (*b.*), through which passes a dark brown stalk or *peduncle* (Fig. 674, *B*, *pd.*) of horny consistency. In the natural state the peduncle is attached to a rock or other support, and the animal lies with the ventral valve uppermost and with the valves gaping slightly. The pointed or peduncular end of the shell is considered to be posterior in position, the opposite end or gape anterior.

It will be convenient to consider the shell first. Both valves are deeply concavo-convex, of a pinkish or brown colour outside, white within. The ventral valve (Fig. 673), as already stated, is produced posteriorly into a beak (*b.*), terminating in a foramen (*f.*) for the peduncle. The distal margin of the foramen is left incomplete by the shell proper, but is closed by a small double plate, the *deltidium* (*d.*). Immediately anterior to the beak is the curved *hinge-line* along which the valve articulates with its fellow, and just anterior to the hinge-line the inner surface of the shell is produced into a pair of massive, irregular *hinge-teeth* (*t.*). On the inner surface of the valve, towards its posterior

end, are certain shallow depressions marking the attachments of muscles (*ad. m.*, *d. m.*).

The dorsal valve (*D*) has no beak, but its posterior edge forms a hinge-line which is produced in the middle into a strong *cardinal process* (*c. p.*) with a curiously folded surface: when the two valves are in position this process fits between the hinge-teeth of the ventral valve, the hinge-teeth in their turn

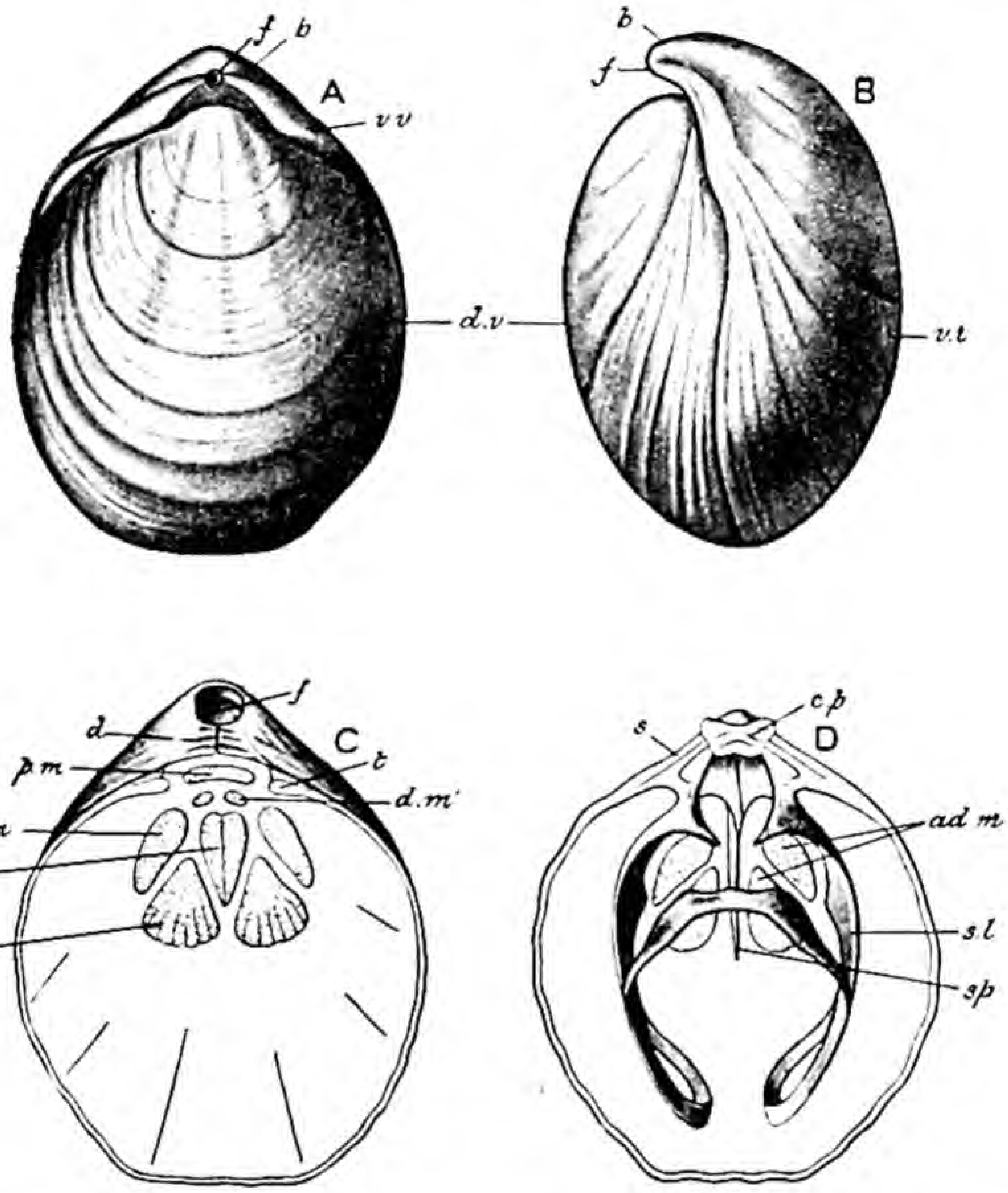


FIG. 673.—**Magellania flavescens.** *A*, the entire shell from the dorsal aspect, and *B*, from the left side; *C*, interior of ventral valve, and *D*, of dorsal valve. *ad. m.* adductor impressions; *b.* beak; *c. p.* cardinal process; *d.* deltidium; *d. m.* divaricator impressions; *d. v.* dorsal valve; *f.* foramen; *p. m.* protractor impressions; *s.* tooth-socket; *s. l.* shelly loop; *sp.* septum; *t.* hinge-tooth; *v. aj. m.* adjustor impressions; *v. v.* ventral valve. (After Davidson.)

being received into depressions (*s*). placed on each side of the cardinal process. The inner surface of the dorsal valve is produced into a median ridge or *septum* (*sp.*), continuous posteriorly with the cardinal process, and attached on either side of the base of the latter are the two ends of a delicate calcareous ribbon, the *shelly loop* (*s. l.*), which projects freely into the cavity enclosed between the two valves, and has the form of a simple loop bent upon itself. The inside of the dorsal valve also has muscular impressions.

Externally both valves present a series of concentric markings parallel with the edge or gape: these are lines of growth, the shell being built up by new layers being deposited within those previously formed, and projecting beyond them so as to form a series of outcrops.

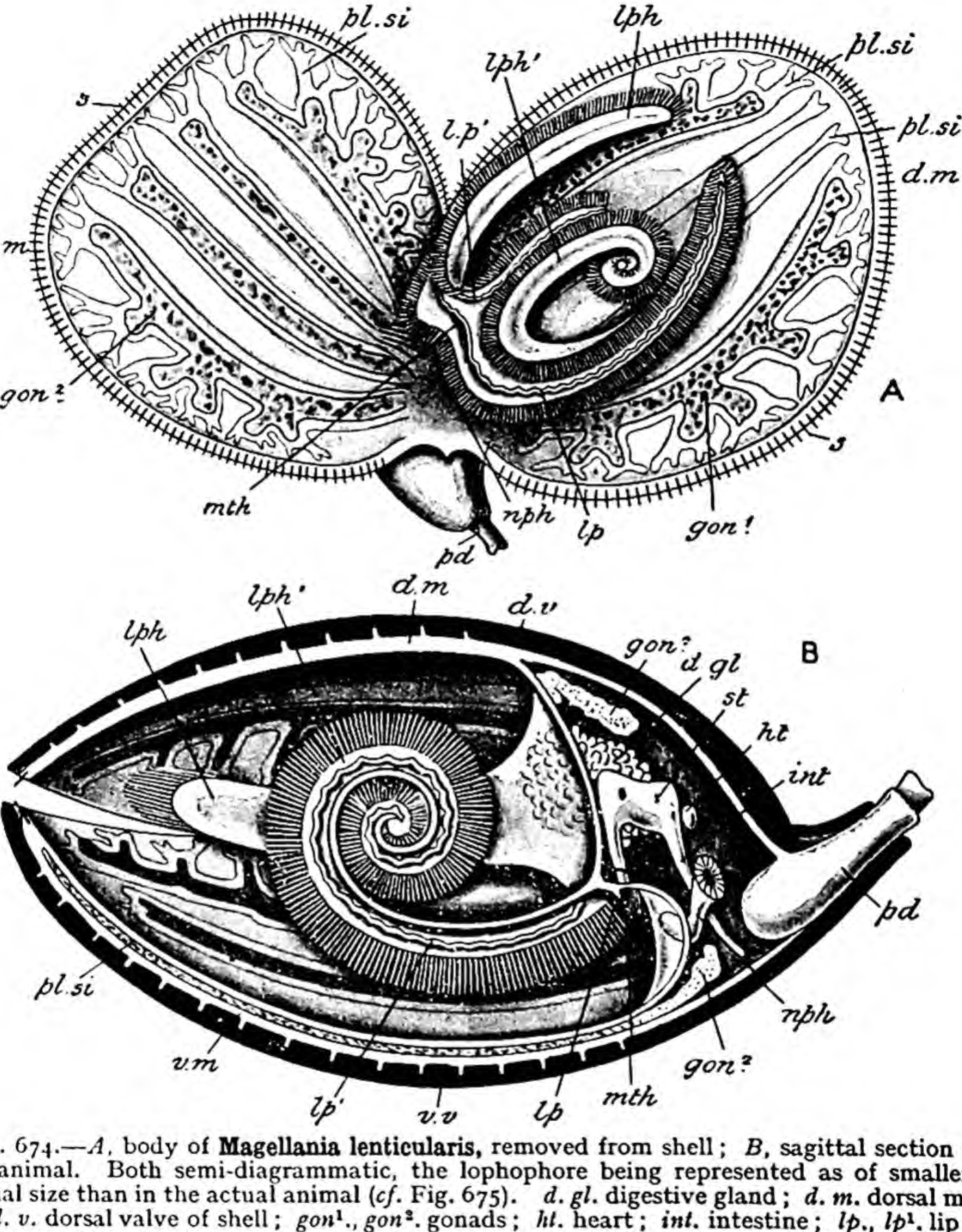


FIG. 674.—*A*, body of **Magellania lenticularis,** removed from shell; *B*, sagittal section of the entire animal. Both semi-diagrammatic, the lophophore being represented as of smaller proportional size than in the actual animal (*cf.* Fig. 675). *d. gl.* digestive gland; *d. m.* dorsal mantle-lobe; *d. v.* dorsal valve of shell; *gon*[1]., *gon*[2]. gonads; *ht.* heart; *int.* intestine; *lp.*, *lp*[1]. lip; *lph.* lophophore; *lph*[1]. its coiled process; *mth.* mouth; *nph.* in *B*, excretory duct, in *A*, excretory aperture; *pd.* peduncle; *pl. si.* pallial sinuses; *s.* setæ; *st.* stomach; *v. m.* ventral lobe of mantle; *v. v.* ventral valve of shell.

Microscopically the shell consists of prismatic rods or spicules of carbonate of lime, placed obliquely to the surface and separated from one another by a

thin layer of membrane. It is also traversed, perpendicularly to the surface, by delicate tubules which begin on the inner surface in microscopic apertures and extend to within a short distance of the outer surface.

The actual **body** of the animal (Fig. 674, *B*) lies at the posterior end of the shell, occupying not more than a third of the space enclosed between the two valves: it is consequently more or less wedge-shaped in form, and presents dorsal and ventral surfaces in contact with the two valves, and an anterior surface looking towards the gape. The dorsal is of greater extent than the ventral surface, so that the anterior surface is placed obliquely.

The dorsal and ventral regions are continued each into a flat reduplication of the body-wall, closely applied to the corresponding valve and containing a prolongation of the cœlome. The two flaps thus formed are the *dorsal* (*d. m.*) and *ventral* (*v. m.*) *mantle-lobes*. They are fringed with minute setæ (*s.*) lodged in muscular sacs, like those of Chætopods (*vide* Sect. VII.), and give off from their outer surfaces hollow processes which extend into the tubules of the shell mentioned above.

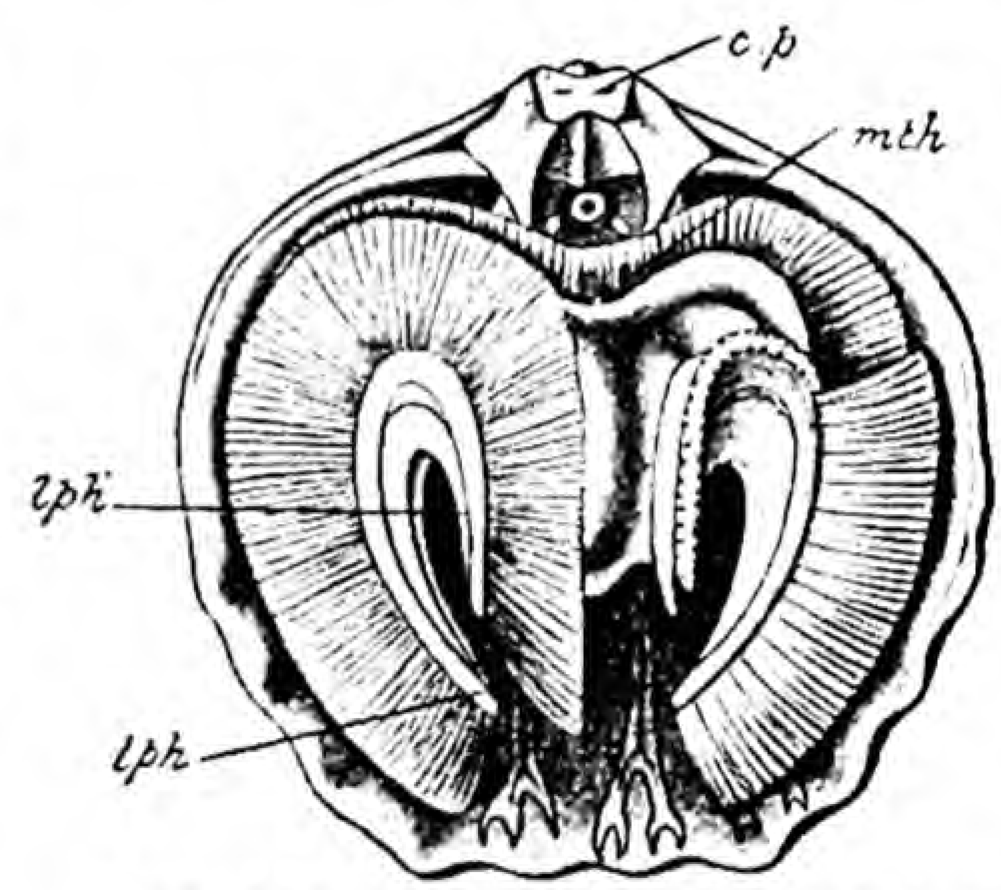


Fig. 675.—**Magellania flavescens,** the ventral valve removed. *c. p.* cardinal process; *lph.* arm of lophophore; *lph*[1]. its coiled process, with the tentacles removed on the right side; *mth.* mouth. (After Davidson.)

The large wedge-shaped space or *mantle-cavity*, bounded by the mantle-lobes above and below, and behind by the anterior surface of the body, is occupied by a huge and complex *lophophore* (Figs. 674 and 675, *lph.*), which springs from the anterior surface of the body, and, like that of the fresh-water Bryozoa and of Phoronis, has the general form of a horse-shoe. It is, however, peculiarly modified: the two limbs of the horse-shoe curve towards one another so as to adapt themselves to the mantle-cavity; and the middle of the concave edge, which is dorsal in position, is produced into a spirally coiled offshoot (*lph'.*) which lies between the two arms and is coiled towards the dorsal side. The lophophore is hollow, containing a spacious cavity or sinus: its two main arms also receive prolongations of the cœlome into which the digestive glands project: it is fringed throughout its whole extent with long ciliated tentacles which form the outer boundary of a ciliated *food-groove*, bounded on the inner side by a wavy ridge or *lip* (*lp.*, *lp'.*). By the action of the cilia microscopic particles are swept along the food-groove to the mouth.

Digestive Organs.—The *mouth* (*mth.*) is a narrow crescentic aperture situated in the middle of the lophophore, towards its convex or ventral edge, and is bounded dorsally by the lip. It leads into a V-shaped enteric canal which

consists of a *gullet* passing upwards from the mouth, an expanded *stomach*, (*st.*), and a straight *intestine* (*int.*) which extends from the stomach downwards and backwards towards the ventral surface and ends blindly, there being no anus. On each side of the stomach, and opening into it by a duct, is a large, branched *digestive gland* (*d. gl.*). The whole canal is lined with ciliated epithelium.

The **body-wall** consists externally of an epidermis formed of a single layer of cells, then of a layer of connective tissue, of a cartilaginous consistency in many parts, and finally of a ciliated cœlomic epithelium lining the body-cavity.

The **muscular system** (Fig. 676) is well developed. Two large *adductor muscles* (*ad. m.*) arise on each side from the dorsal valve, and passing downwards, unite with one another so as to have a single insertion on the ventral valve: their action is to approximate the valves and so to close the shell. A large

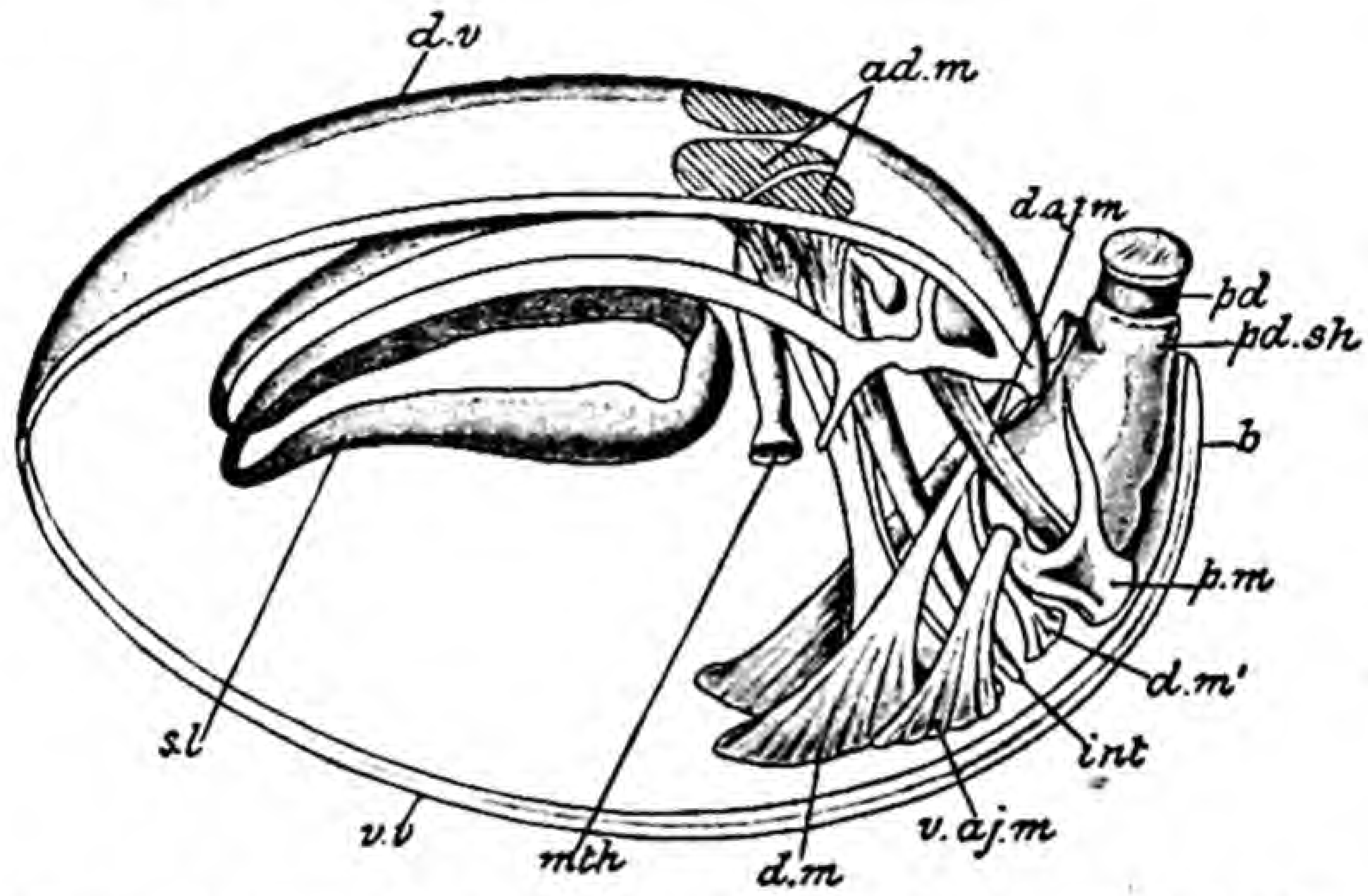


FIG. 676.—Muscular system of **Magellania.** *ad. m.* adductors; *b.* beak; *d. aj. m.* dorsal adjustors; *d. m.*, *d. m'.* divaricators; *d. v.* dorsal valve; *int.* intestine; *mth.* mouth; *pd.* peduncle; *pd. sh.* sheath of peduncle; *p. m.* protractor; *s. l.* shelly loop; *v. aj. m.* ventral adjustors; *v. v.* ventral valve. (After Hancock.)

and a small pair of *divaricators* (*d. m.*, *d. m'.*) arise from the ventral valves, and are inserted into the cardinal process, which they depress: as this process is situated posteriorly to the hinge-line, its depression raises the rest of the dorsal valve and so opens the shell. Two pairs of muscles arising, one from the ventral, the other from the dorsal valve, and inserted into the peduncle, are called *adjustors* (*aj. m.*): the peduncle being fixed, they serve to alter or adjust the position of the animal as a whole by turning it in various directions.

The **cœlome** is a spacious cavity more or less encroached upon by the muscles and other organs, and traversed by sheets and bands of membrane which connect the enteric canal with the body-wall, and thus act as mesenteries. The cœlome is continued into each of the mantle-lobes in the form of four canals or *pallial sinuses* (Fig. 674, *pl. si.*), the two outer of which are extensively branched.

Blood-system.—Attached to the posterior region of the stomach is a small, almost globular sac (*h*), which has been proved to be contractile and is to be considered as a *heart*. Vessels have been traced from it to various parts of the body, but the relations of the whole circulatory system and the course of the circulation are very imperfectly known.

The **excretory organs** consist of a pair of very large excretory ducts (*nph.*) lying one on each side of the intestine. Each is funnel-shaped, having a wide inner opening or *nephrostome*, with plaited walls, opening into the cœlome, and

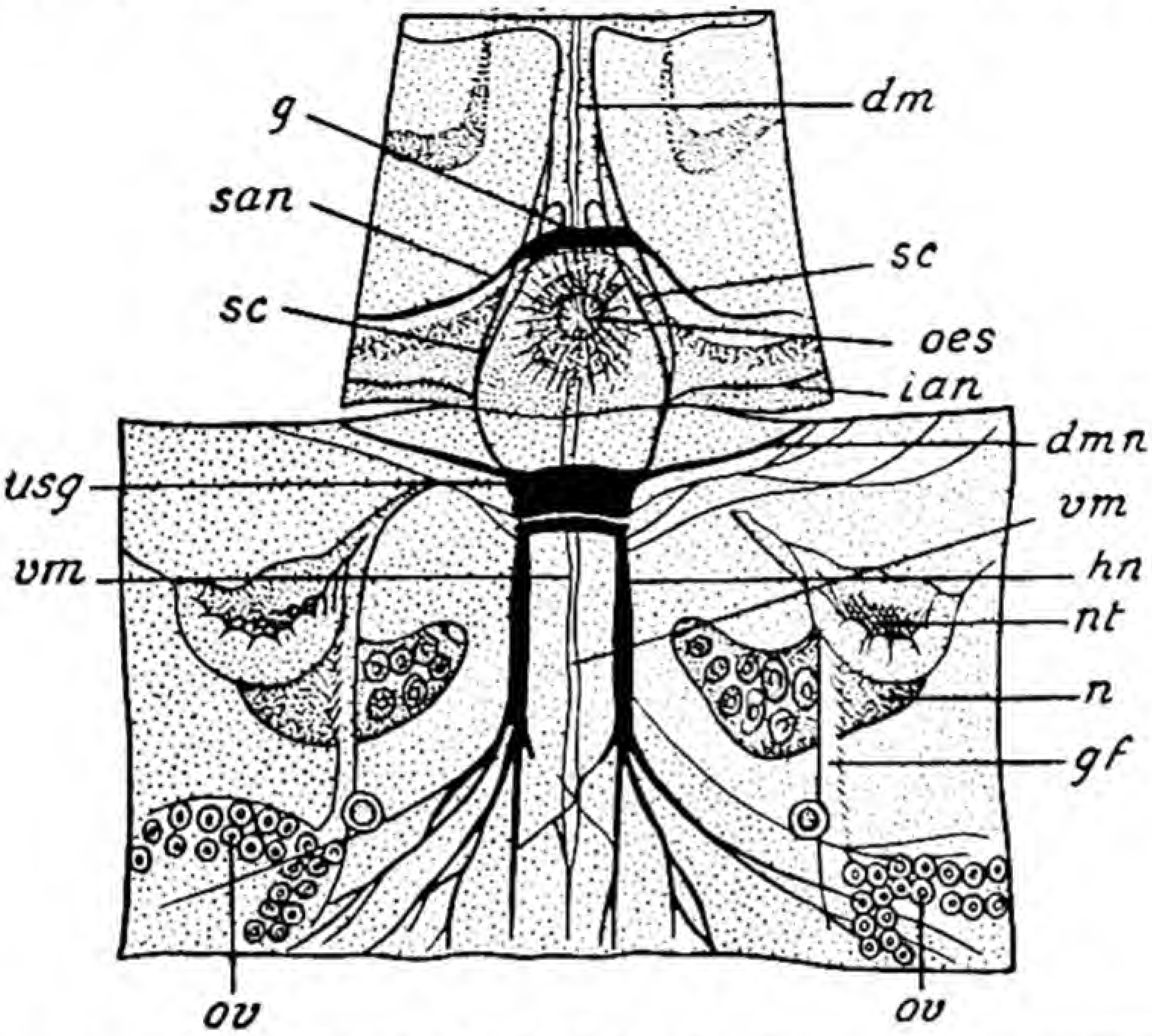


FIG. 677.—Anterior body-wall of **Terebratula,** to show nervous system, etc. *dm.* dorsal mesentery; *g.* brain; *gf.* genital folds; *n.* excretory organ; *nt.* nephrostome; *œs.* gullet; *ov.* ovary; *sc.* œsophageal connective; *usg.* infra-œsophageal ganglion; *vm.* ventral mesentery; *dmn., hn., ian., san.* nerves. (From Lang's *Comparative Anatomy*, after van Bemmelen.)

a narrow, curved, outer portion which opens into the mantle-cavity not far from the mouth. The excretory ducts act also as gonoducts.

The **nervous system** (Fig. 677) is a ring round the gullet presenting supra- (*g.*) and infra- (*usg.*) œsophageal swellings or ganglia, of which the infra-œsophageal is the larger. Nerves are given off to the mantle, lophophore, etc. No special sense-organs are known.

Reproductive Organs.—The sexes are separate. There are two pairs of gonads (Fig. 674, *gon.*), one dorsal and one ventral, in the form of irregular organs sending off branches into the pallial sinuses.

2. Distinctive Characters and Classification.

In the Brachiopoda the body is enclosed in a shell formed of two parts or valves which are respectively dorsal and ventral in position. The body occupies only a

small portion of the space enclosed by the shell, and is usually attached to foreign objects by a posteriorly placed stalk or peduncle ; it gives off dorsal and ventral reduplications, the mantle-lobes, which line the valves of the shell and enclose a large mantle-cavity. From the anterior surface of the body is given off a lophophore which surrounds the mouth, and is beset with ciliated tentacles. There is a ridge-like pre-oral lip which is continued on to the lophophore. The enteric canal is usually V-shaped, and is divisible into gullet, stomach, and intestine ; there is a pair of digestive glands. The cœlome is spacious, and is continued into the mantle-lobes. A heart is usually present, attached to the stomach. The excretory organs are one or two pairs of wide funnelled ducts which act also as gonoducts. The nervous system is a ganglionated circum-œsophageal ring ; sense-organs are usually absent in the adult. The sexes are separate or united. Development is accompanied by a metamorphosis.

The class is divided into two orders :—

ORDER 1.—ECARDINES (INARTICULATA).

Brachiopoda in which the shell is mainly composed of chitinoid material with a varying proportion of calcified substance : the valves are not united by a hinge, and there is no shelly loop for the support of the lophophore. An anus is present.

Including *Lingula*, *Crania*, *Discina* (all in Fig. 678), and others.

ORDER 2.—TESTICARDINES (ARTICULATA).

Brachiopoda in which the shell is formed of oblique prisms or spicules of calcium carbonate : the two valves unite by a definite hinge, and there is usually a shelly loop, for the support of the lophophore, developed in connection with the dorsal valve. The intestine ends blindly.

Including *Rhynchonella*, *Magellania* (*Waldheimia*) (Fig. 674), *Terebratula* (*Liothyrina*), *Cistella* (*Argiope*), and others.

3. GENERAL ORGANIZATION.

The **shell** presents two distinct types : in the Testicardines, the order to which Magellania belongs, the dorsal and ventral valves are dissimilar, the dorsal valve having a cardinal process and usually a shelly loop, the ventral a spout-like beak for the peduncle ; while in the Ecardines, of which Lingula is a good example (Fig. 678, *A*), the two valves are nearly alike, and there is no shelly loop and no beak. These differences are accompanied by differences in microscopic structure ; in the Testicardines the shell is dense and stony, and is formed of obliquely placed calcareous prisms, while in the Ecardines it has no prismatic structure, but usually consists of a chitinoid material more or less

strengthened by calcareous spicules, or of alternate chitinoid and calcareous layers. A system of tubules, such as that described above in the case of the example, occurs in many cases. Among the Testicardines the loop may be absent; when present, it varies greatly in form and size, being sometimes very small and simple (Fig. 678, *C*, *D*), sometimes bent upon itself, as in Magellania, sometimes attached to the septum or to the interior of the dorsal valve (*E*), sometimes, as in the extinct *Spirifera*, represented by a complex double spiral (*F*), sometimes reduced to short, paired rods springing from the septum (*G*).

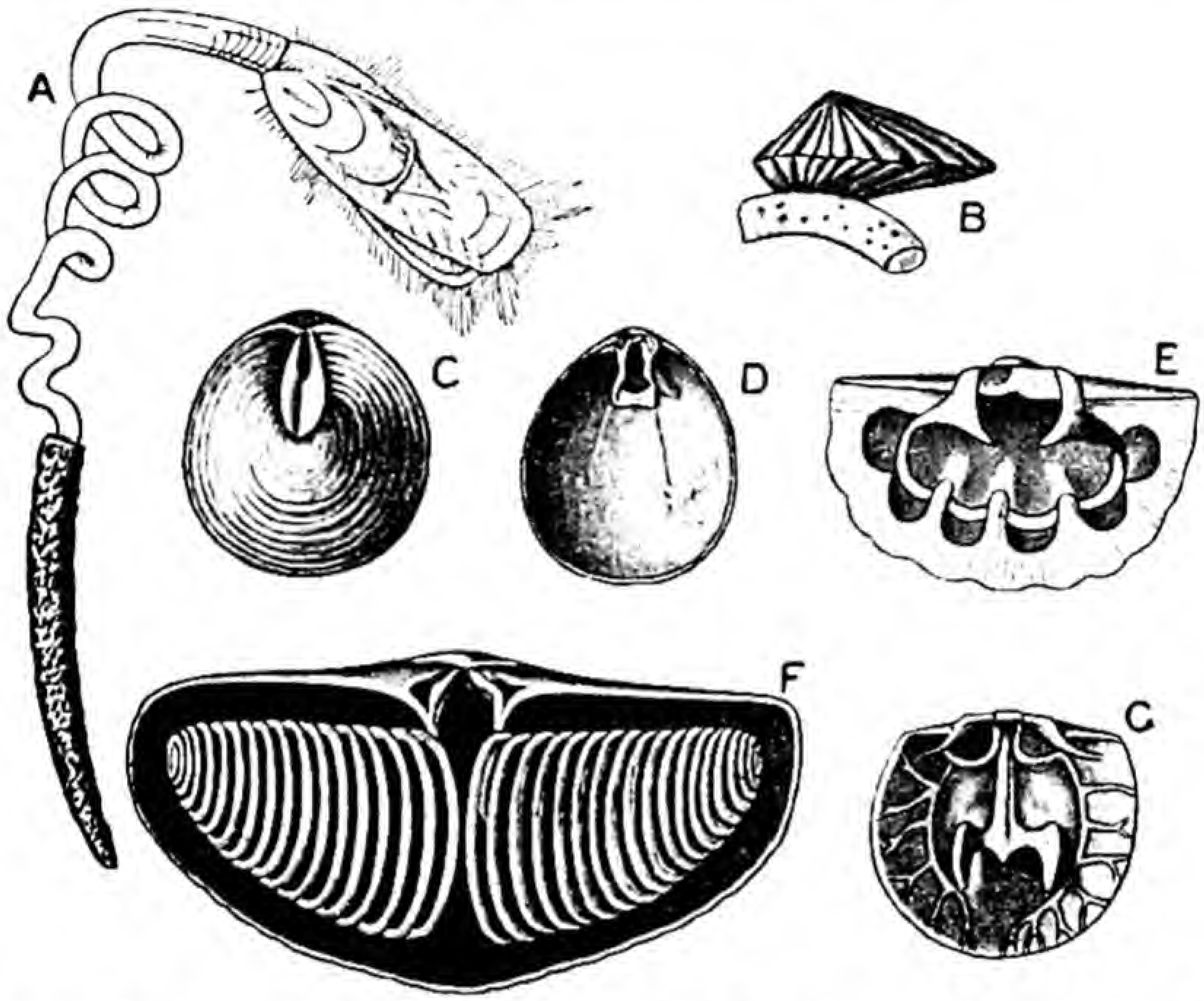


FIG. 678.—Typical Brachiopoda. *A*, **Lingula**; *B*, **Crania**; *C*, **Discina**; *D*, **Terebratula**; *E*, **Cistella**; *F*, **Spirifera**; *G*, **Kraussina**. (After Bronn.)

The shell is secreted partly by the general surface of the body, partly by the folds and papillæ of the mantle.

In some cases **spicules** occur scattered through the soft parts.

The majority of both orders are attached by a longer or shorter **peduncle** which passes between the proximal ends of the valves in Lingula (Fig. 678, *A*), through a perforation in the ventral valve in Discina (*C*), and through a foramen in the spout-like posterior end of the ventral valve in the Testicardines. Crania (*B*) has the ventral valve fixed directly to foreign objects, the peduncle being absent.

The **lophophore** is found in its simplest form in *Cistella* (Fig. 679, *A*), in which it is a horse-shoe-shaped disc with very short arms, attached to the dorsal mantle-lobe, of which it is a prolongation, and surrounded with flexible tentacles which project between the valves. From this the lophophore of

Magellania, which may be considered as typical for the Testicardines, is easily derived by an increase in size, and by the prolongation of the middle region of the concave edge into a coiled offshoot. In the Ecardines (*C*), and in Rhynchonella (*B*) among the Testicardines, each arm of the horse-shoe is coiled into a conical spiral, which in some cases can be protruded between the valves. In all cases a section of the arm shows the same general character, with a groove, one of the lips of which is a simple ridge, while the other is the row of tentacles.

The most noteworthy point about the **muscular system** is the fact that the

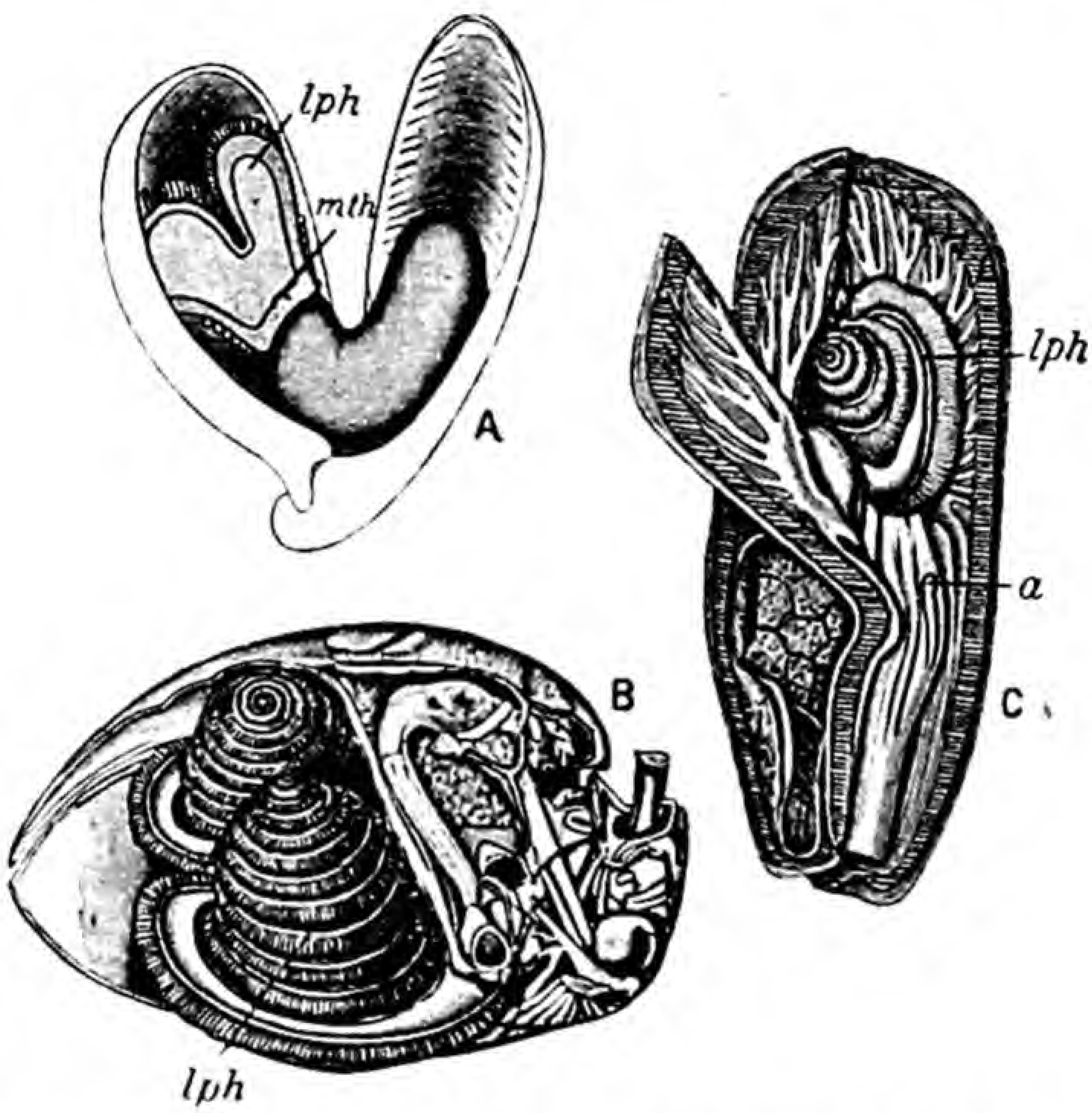


FIG. 679.—Dissections of *A*, **Cistella**; *B*, **Rhynchonella**; and *C*, **Lingula**. *a*. anus; *lph*. lophophore; *mth*. mouth. (After Schulgin and Hancock.)

shell is both opened and closed by muscular action. The dorsal valve may be taken to represent a lever of which the hinge-line is the fulcrum, the cardinal process the short arm, and the main portion of the valve the long arm. The mode of action of the three principal sets of muscles—adductors, divaricators and adjustors—has been described in the account of the example. In Lingula there is a very complex muscular system by means of which the valves can be rubbed upon one another, or moved laterally as well as opened and shut.

In the Testicardines the **enteric canal** is V-shaped, as in Magellania, the intestine being straight or nearly so, and ending blindly. In the Ecardines, on the other hand, the intestine is usually coiled, and always ends in an anus (Fig. 679, *C*, *a*), which generally opens into the mantle-cavity, but in one

genus (Crania) into a pouch or sinus at the posterior end of the body between the valves.

A **heart** is usually present, but the function of blood is performed mainly by the cœlomic fluid, which is propelled by the cilia lining that cavity, and circulates both in the cœlome itself and in the pallial sinuses, each sinus presenting—in Lingula at least—both an outgoing and an ingoing current.

A single pair of **excretory ducts,** resembling those of Magellania, occurs in all known genera except Rhynchonella, in which there are two pairs, one dorsal and one ventral. Besides discharging an excretory function they act as gonoducts.

The **nervous system** always takes the form of a circum-œsophageal ring with ganglionic enlargements, the largest of which is ventral or sub-œsophageal in position. Statocysts have been described in Lingula, rudimentary eyes in Megerlia, and patches of sensory epithelium in Cistella: with these exceptions sensory organs are unknown.

There are usually four **gonads,** two dorsal and two ventral, sending prolongations into the pallial sinuses. The sexes are generally distinct.

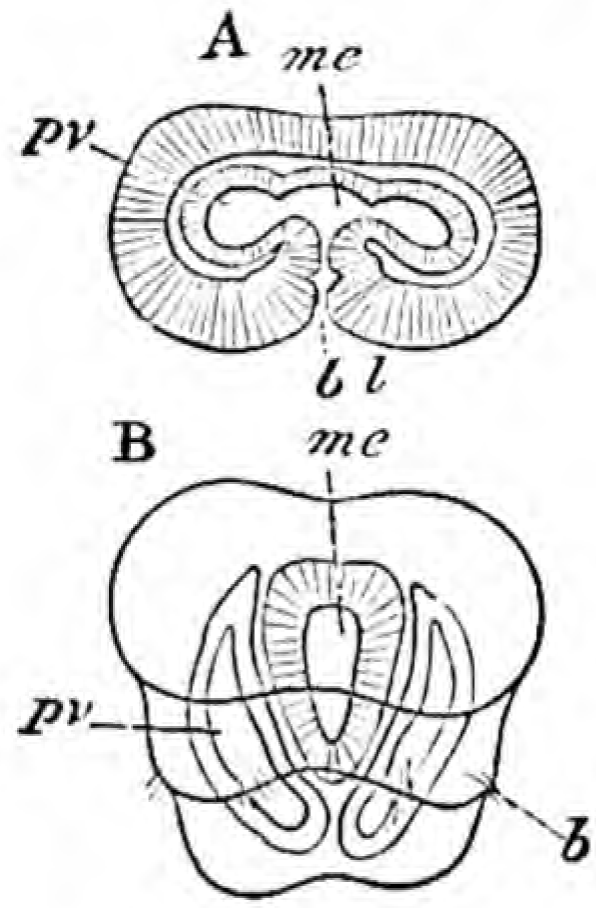


FIG. 680.—Two stages in the development of **Cistella** (*Argiope*). *b*. provisional setæ; *bl*. blastopore; *me*. mesenteron; *pv*. cœlomic pouches. (From Balfour's *Embryology*, after Kowalevsky.

The **embryology** and **larval history** of the Brachiopoda have been worked out only in four genera belonging to the Testicardines and one (Lingula) belonging to the Ecardines. The following are the chief general characteristics of the development in the former. In three of the four genera referred to the earlier stages are passed through in brood-pouches; in the fourth the eggs are only attached temporarily to the setæ of the parent and become free in a comparatively immature condition. Cleavage is regular and complete, and results in the formation of a ciliated blastula, the wall of which is composed of cells of like character throughout. This is converted into a gastrula by invagination (Fig. 680, *A*): the blastopore narrows to a slit and gradually completely closes. The stomodæum arises as an invagination of the surface ectoderm apparently in the position of the anterior end of the former blastopore. An ectodermal thickening in front forms the *apical plate* from which the supra-œsophageal ganglion is derived, and a second thickening behind the mouth on the ventral surface subsequently gives origin to the infra-œsophageal ganglion. Meanwhile the cœlome originates in a pair of sacs (Fig. 680, *pv*.), or a single sac subsequently dividing into two—the *cœlomic pouches*—growing out from the archenteron, and eventually becoming completely closed off from it to give rise to the cœlome, which is thus of the enterocœle-type as regards its derivation. A groove, the *mantle-groove*, running transversely divides the embryo into two regions, a broad anterior and a narrower posterior. Folds which are formed

in front of the mantle-groove are the beginnings of the dorsal and ventral mantle-lobes. A groove which appears in front of these separates off a head segment from the rest, and the embryo is now divided into three segments or regions—*head region, body-* or *mantle-region*, and *foot-* or *peduncle-region* (Fig. 681). The mantle-lobes increase in size and grow backwards over the peduncular region: in them are developed four groups of *provisional setæ* which project backwards (Fig. 681): in Cistella, in which there are no setæ in the adult, these are thrown off subsequently: in the genera in which setæ are present in the adult they are also thrown off, but are replaced later by the permanent setæ. The head-region has in the meantime become broadened out and in Cistella soon assumes the form of an umbrella-shaped disc bordered with cilia and usually bearing eye-spots (Fig. 682, *A*), and sometimes an apical tuft of long cilia. In this condition the larva swims freely like a trochophore. After a time it comes to rest and fixes itself by the peduncular segment. The mantle-folds become reflexed so as to point forwards instead of backwards, thus leaving the peduncular region exposed and covering the head-region

FIG. 681.—Young larva of **Cistella (Argiope)**, with the three segments, two eye-spots, and two bundles of setæ. (From the *Cambridge Natural History*, after Kowalevsky.)

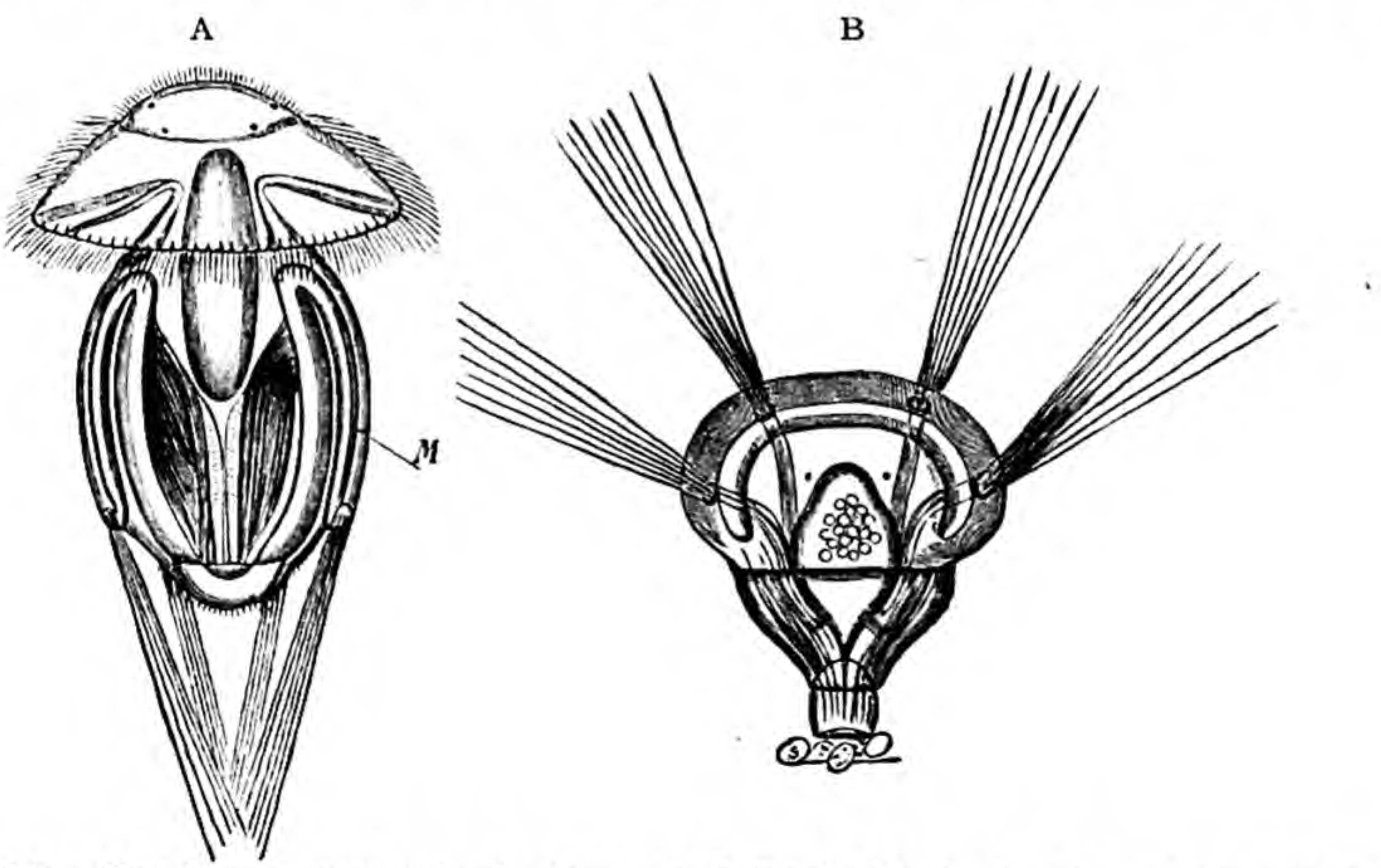


FIG. 682.—Two later stages in the development of **Cistella (Argiope)**. *A*. free-swimming; *B*. after fixation; *M*. mantle. (From Claus, Grobben and Kühn's *Lehrbuch der Zoologie* (Julius Springer), after Kowalevsky.)

(Fig. 682, *B*). The umbrella-like head-region decreases in size, and perhaps forms the lip, which is at first confined to the part immediately dorsal to the

mouth. The lophophore appears at first on the inner surface of the dorsal mantle-lobe, but gradually extends and surrounds the mouth; in its earlier stages it is circular, but afterwards assumes the horse-shoe form by sending out paired extensions. In genera with a complex lophophore, like Magellania, this organ has at first a simple horse-shoe form (Fig. 683, *lph.*). A shell is secreted by the mantle-lobes, and the peduncular region becomes the peduncle of the adult.

The development of Lingula (Ecardines) differs somewhat widely from that of the Testicardines. There is no division by definite constrictions into three regions. The head-region does not expand to the same extent: it early develops elevations which are the rudiments of the first-formed tentacles. The ridge from which the mantle-lobes are developed grows forwards from the outset. The cœlome is not formed by outgrowth from the archenteron, but appears as a pair of cavities in a pair of masses of mesoderm-cells which are at first solid proliferations from the wall of the latter: in other words the cœlome is not formed as an enterocœle but as a schizocœle.

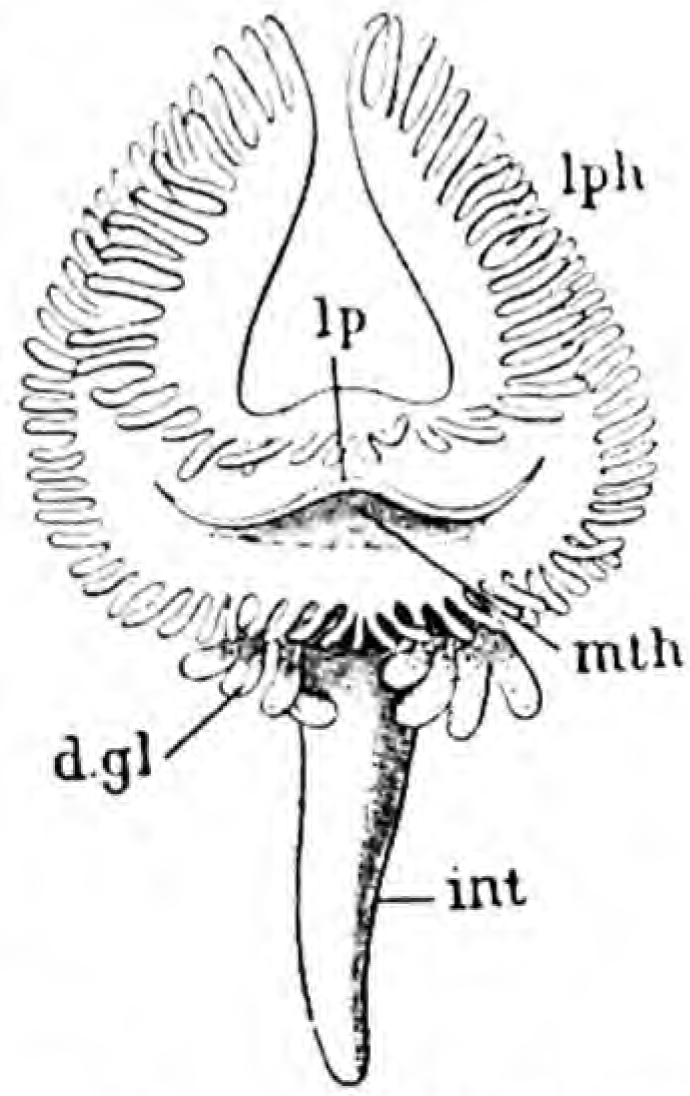


FIG. 683.—Lophophore of embryo of **Terebratulina.** *d. gl.* digestive gland; *int.* intestine; *lp.* lip; *lph.* lophophore; *mth.* mouth. (From Korschelt and Heider, after Morse.)

Distribution.—The Brachiopoda are all marine. They are widely distributed geographically, and live at various depths—from between tide-marks to 2,900 fathoms. At the present day the class includes only about 20 genera and 100 species, but in past times the case was very different. Brachiopods appear first in the lower Cambrian rocks, where genera hardly differing from the existing Lingula and Discina are found. No more striking examples can be adduced of persistent types—organisms which have existed almost unchanged for the vast period during which the whole of the fossiliferous rocks have been in process of formation. More than twice as many genera are known from the Palæozoic rocks as from the Mesozoic, and many more from the Mesozoic than from the Cainozoic and Recent periods. Obviously the group is tending, though slowly, towards extinction.

Researches on fossil and recent forms have shown the Brachiopoda to illustrate, in a remarkable manner, the recapitulation theory already referred to: the theory, that is, that ontogeny or individual development is a more or less modified recapitulation of phylogeny or ancestral development. It has been shown that there is a striking and almost complete parallelism between the stages in the development of the shelly loop in such highly organized forms as Magellania and the entire series of articulated Brachiopods from those with the simplest to those with the most complex loop.

THE CHÆTOGNATHA.

The Chætognatha are an isolated group whose position in the animal kingdom is still completely obscure. The group contains only three genera (*Sagitta, Eukrohnia*, and *Spadella*) of curious arrow-shaped pelagic animals.

External Characters.—The body (Fig. 684) is elongated and nearly cylindrical, and is divided into *head, trunk*, and *tail*, the head being marked off by its somewhat rounded form, while the junction of trunk and tail is indicated by the ventrally placed anus (*a.*). The tail bears a horizontal expansion, or *caudal fin* (*t. f.*), and there are also horizontal *lateral fins* (*l. f.*)—a single pair in Spadella, two pairs in Sagitta.

Body-wall.—The outer layer of the body-wall is formed by an epidermis or deric epithelium which, in certain regions, is formed of several layers of epithelial cells. It secretes a structureless cuticle. Next comes a delicate *basement membrane*, and then a layer of muscles (*m.*), the fibres of which are striated and disposed longitudinally in four bands—two dorso-lateral and two ventro-lateral—an arrangement which recalls the muscular arrangement in the Nematoda.

Enteric Canal.—The mouth (Fig. 684, *m.*) is a longitudinal slit-like aperture on the ventral surface of the head; on either side of it are several sickle-shaped chitinoid hooks (Fig. 686, *h.*) which are moved by muscles in a horizontal plane and serve as jaws. The anterior region of the head also bears spines, and is strengthened by chitinoid plates and partly covered by a hood-like fold of the integument.

The mouth leads by a muscular *pharynx* or stomodæum into a straight *intestine* (Fig. 684, *int.*), which extends through the trunk and opens by the anus (*a.*) at the junction of trunk and tail.

Cœlome.—At the junction of the head with the trunk, and of the trunk with the tail, are transverse partitions or *septa*, dividing the cœlome into compartments. The trunk region of that cavity is further subdivided by two longitudinal partitions, the *dorsal* and *ventral mesenteries*, which respectively connect the dorsal and ventral surfaces of the intestine with the body-wall: the tail-region of the cœlome is similarly divided into right and left chambers by a longitudinal vertical partition.

There is no trace of **vascular system** or of **excretory canals.** The **nervous system**, on the other hand, is well developed. On the dorsal side of the pharynx is a comparatively large *brain* (Fig. 686, *br.*), which sends off on each side a long nerve-cord, the *œsophageal connective* (*œs. c.*). The two connectives sweep round the enteric canal and unite on the ventral surface, not far from the middle of the trunk, in an elongated *ventral ganglion* (Fig. 684, *v. g.*), from which numerous nerves are given off. The brain sends nerves to the eyes

(Fig. 686, *o. n.*) and to the olfactory organs (*o. o.*), and is also connected with two pairs of ganglia in the head, which lie deeply sunk in the mesoderm: all the rest of the nervous system retains its primitive connection with the ectoderm.

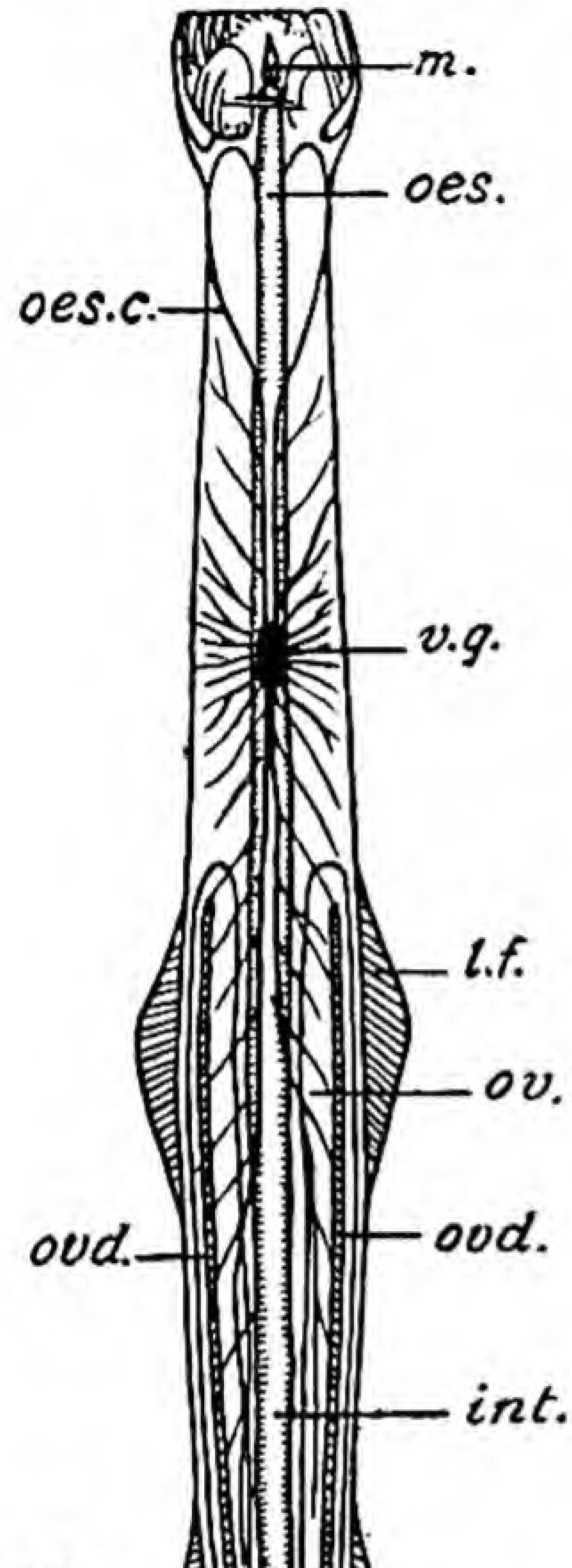


FIG. 684.—**Sagitta hexaptera,** from the ventral aspect. *a.* anus; *f. a.* female aperture; *int.* intestine; *l. f.* lateral fins; *m.* mouth; *œs.* œsophagus; *œs. c.* œsophageal connective; *ov.* ovary; *ovd.* oviduct; *t. c.* tail-cavity; *tes.* testis; *t. f.* tail-fin; *v. d.* vas deferens; *v. g.* ventral ganglion; *v. s.* vesicula seminalis. (From Lang's *Comparative Anatomy*, after Hertwig.)

Sense-organs.—On the surface of the body are numerous little papillæ carrying stiff bristle-like processes, and probably serving as organs of touch. There are two eyes (Fig. 687), situated one on each side of the dorsal surface of the head: each is globular and consists of five *pigment-cup-ocelli* closely applied to one another with their pigmented walls. To each cup belongs a group of visual cells ending in rods which are connected with the brain by fibres of the optic nerves. Behind the head is a ring-like structure, of the nature of an annular ridge of peculiarly modified and in part ciliated cells (Fig. 686, *o. o.*): to this an olfactory function has been assigned.

Reproduction.—The Chætognatha are hermaphrodite. The *ovaries* (Figs. 684, 685, *ov.*) are elongated organs situated one on each side of the trunk-region of the cœlome. In connection with each ovary, there are two co-axial ducts—an inner *sperm duct* (Fig. 685, *sp. d.*), which acts as sperm-pouch and opens on the seminal receptacle—and surrounding it the *oviduct*, which, too, opens on the seminal receptacle. The external aperture of the latter is just in front of the posterior septum. The anterior end of both ducts is blind, and the germ cells actively pass

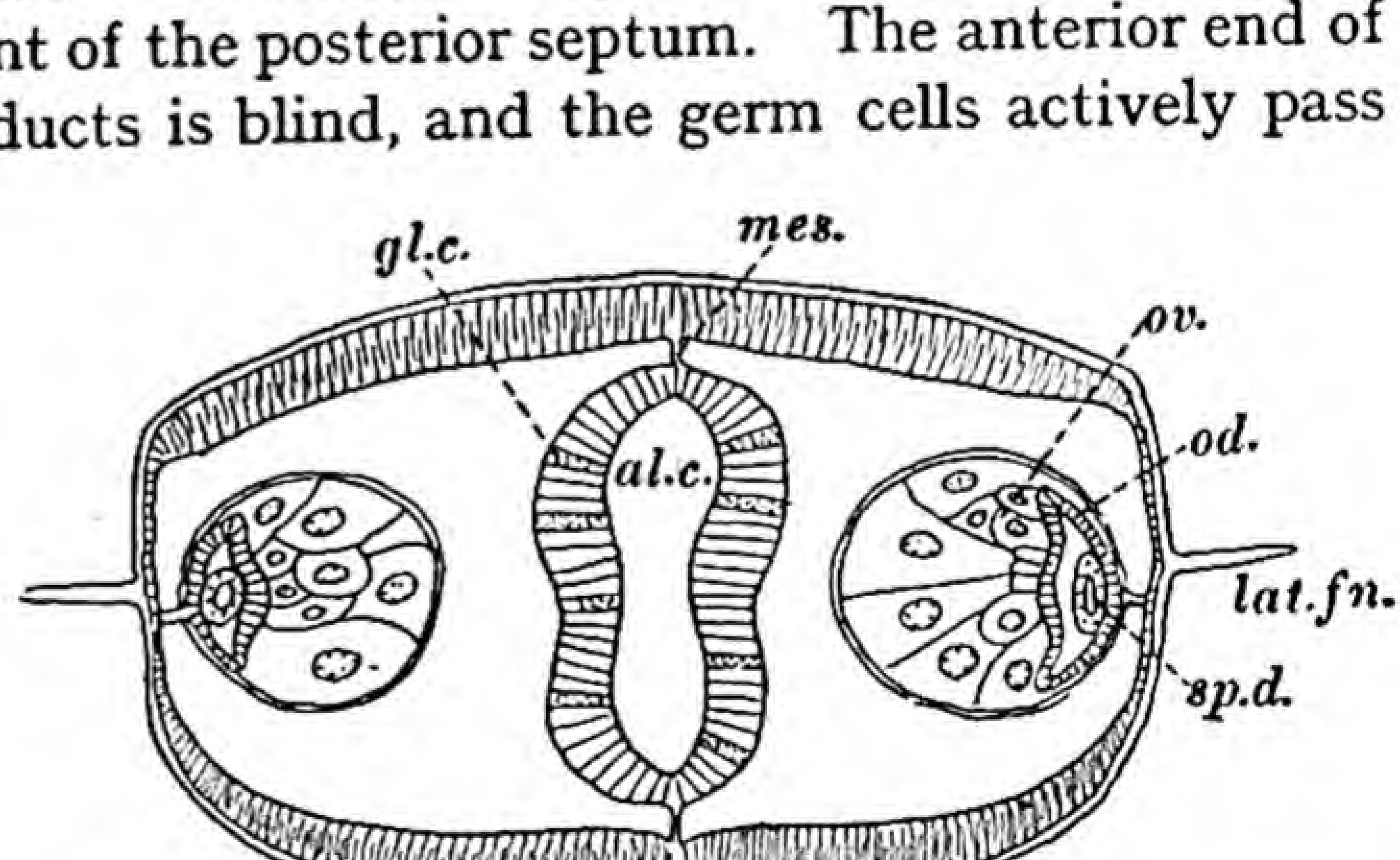


FIG. 685.—**Sagitta bipunctata,** transverse section through the middle of the trunk. *al. c.* intestine; *gl. c.* gland-cells; *lat. fn.* lateral fin; *mes.* mesentery; *od.* oviduct; *ov.* ovary; *sp. d.* sperm-duct. (From Borradaile, Eastham, Potts and Saunders's *The Invertebrata* (University Press, Cambridge), after Burfield.)

through the lining of the ducts. The *testes* (Fig 684, *tes.*) are similarly situated in the tail-region of the cœlome, and have the form of narrow ridges from which immature seminal cells are given off and develop into sperms in the cœlome. The vasa deferentia are delicate tubes (Fig. 684, *v. d.*) opening at one end into the cœlome by a funnel-like extremity, and at the other end dilating into a reservoir or *vesicula seminalis* (*v. s.*), which opens externally in the posterior region of the tail.

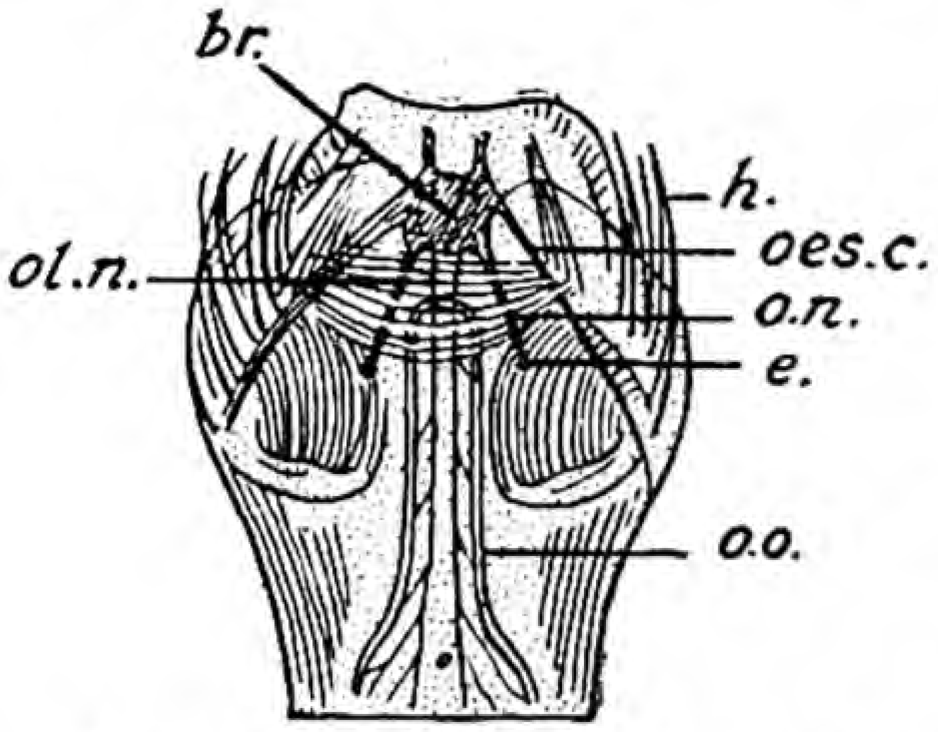


FIG. 686.—Head of **Sagitta bipunctata,** from above. *br.* brain; *e.* eye; *h.* hooks; *œs. c.* œsophageal connective; *ol. n.* olfactory nerve; *o. n.* optic nerve; *o. o.* olfactory organ.

Development.—Internal fertilization takes place, and the fertilized ovum, cleaving completely and regularly, forms a typical gastrula by invagination (Fig. 688, *A*). Two endoderm cells (*g.*) at the anterior end of the archenteron, *i.e.* the end opposite to the blastopore, soon increase greatly in size, and are the rudiments of the gonads. This precocious differentiation of the sex-cells is a point of considerable importance, as will be seen hereafter. Before long these cells migrate into the archenteron and divide, forming a group of four cells (*B*, *g.*), two of which subsequently become the ovaries and two the testes. At the same time two folds of endoderm grow into the archenteron from its anterior end, partly dividing the cavity into three parts—a middle division or

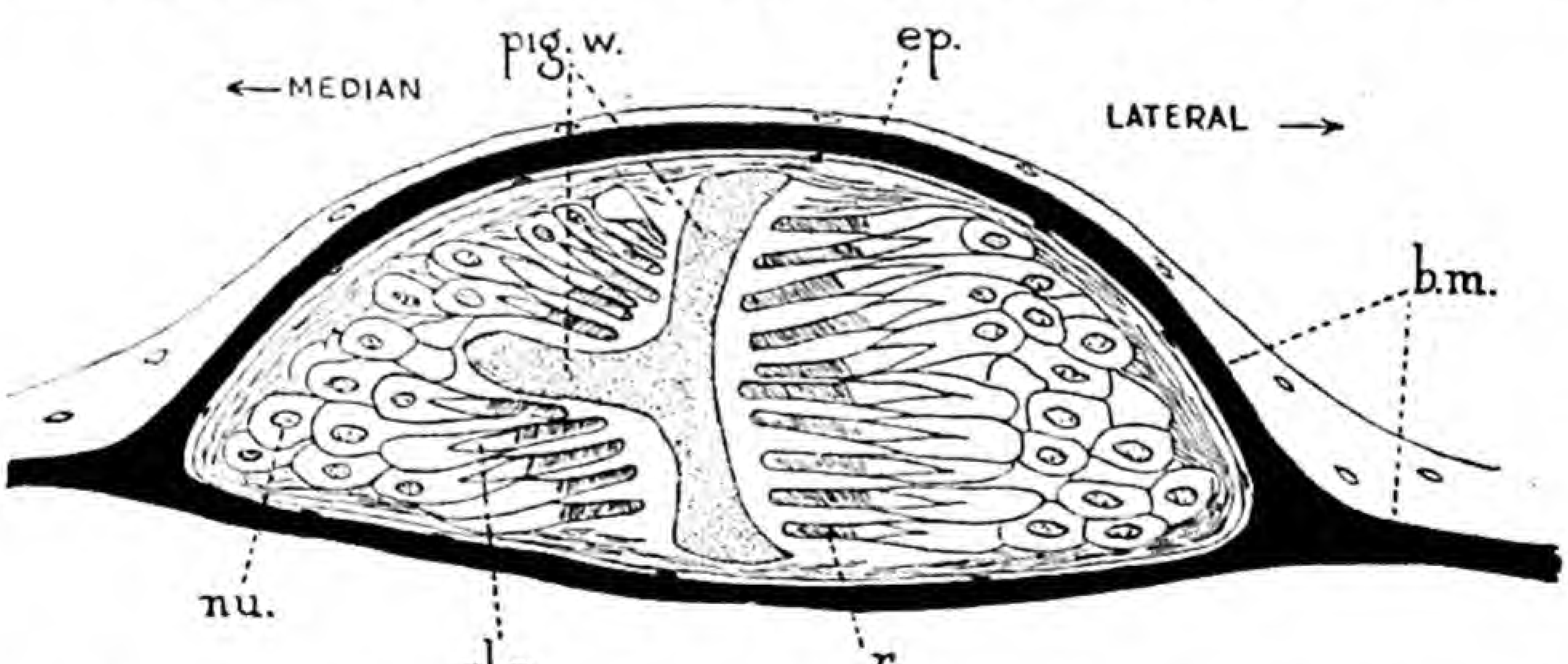


FIG. 687.—Transverse section through an eye of **Sagitta.** *b. m.* basal membrane; *cl. r.* clear area of visual rod; *nu.* nucleus of visual cell; *pig. w.* pigmented wall of ocelli; *r.* rod of visual cell. (From Burfield's *Sagitta* (The University Press of Liverpool, Ltd.).)

mesenteron (*d.*)—the rudiment of the intestine, and two lateral divisions—the cœlomic sacs (*c. s.*)—which give rise to the right and left compartments of the cœlome of the trunk. From the latter are given off in front a pair of small head-cavities. Owing to the rapid elongation of the embryo in the stages

following, all the cavities become for a time obliterated: subsequently the cavities of the enteric canal and cœlomic sacs reappear; the tail-region of the body-cavity is formed from the posterior, undivided portion of the archenteron. The blastopore (*bl.*) now closes and an invagination of ectoderm—the stomodæum (*st.*)—takes place at the anterior end, and finally communicates with the mesenteron.

From this it will be seen that the ectodern of the gastrula gives rise to the

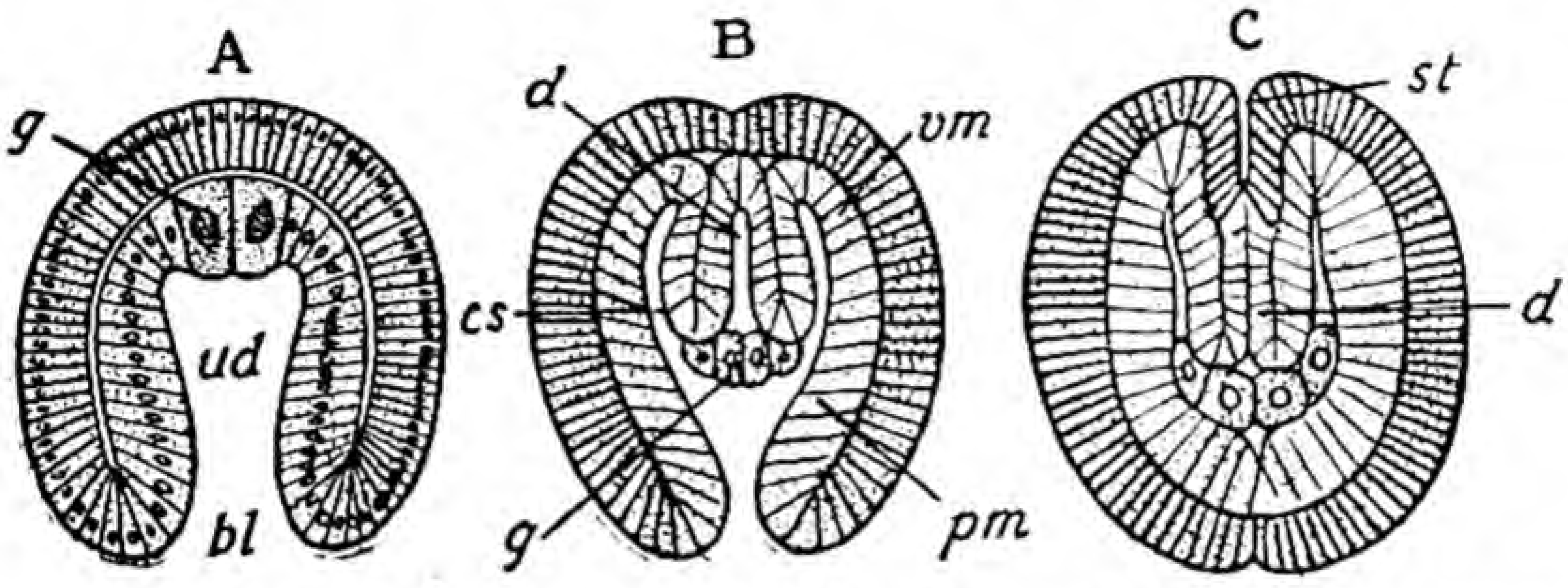


FIG. 688.—Three stages in the development of **Sagitta.** *bl.* blastopore; *cs.* cœlomic sacs; *d.* mesenteron; *g.* sexual cells; *pm.* parietal layer of mesoderm; *st.* stomodæum; *vm.* visceral layer of mesodern. (From Lang's *Comparative Anatomy*, after O. Hertwig.)

deric epithelium of the adult and to the epithelium of the pharynx, which is therefore a stomodæum; from the same layer the nervous system arises at a later stage. The epithelium of the intestine arises from the mesial (inwardly-turned) layers of the two endodermal folds. The muscular layer of the body-wall arises from the rest of the endoderm, *i.e.*, that portion of it which remains in immediate contact with the ectoderm. Thus in Sagitta the mesoderm is entirely derived from the endoderm of the gastrula.

SECTION XI

PHYLUM ECHINODERMATA

THE phylum *Echinodermata* comprises the Starfishes (*Asteroidea*), Brittle-stars (*Ophiuroidea*), Sea-urchins (*Echinoidea*), Sea-cucumbers (*Holothuroidea*), and Feather-stars (*Crinoidea*). All exhibit a radial arrangement of parts, which is recognizable as well in the globular Sea-urchins and elongated Sea-cucumbers as in the star-shaped Starfishes, Brittle-stars and Feather-stars. Another universal feature is the presence of a calcareous exoskeleton, sometimes in the form of definitely shaped plates, which may fit together by their edges so as to form a continuous shell; sometimes merely in the form of scattered particles or spicules. In very many the surface is beset with tubercles or spines, from which feature the name of the phylum is derived. The various systems of organs attain a comparatively high degree of complexity. An extensive cœlome is present, developed in the embryo from hollow outgrowths from the archenteron. The Echinoderms are rarely capable of rapid locomotion, and are sometimes permanently fixed by means of a stalk; they never give rise to colonies by budding. All the members of this phylum are inhabitants of the sea.

1. EXAMPLE OF THE ASTEROIDEA.

A Starfish (*Asterias rubens* or *Anthenea flavescens*).

General External Features of Asterias rubens.—The body of the Starfish is enclosed in a tough, hard integument, containing numerous plates, or *ossicles* as they are termed, of calcareous material. This exoskeleton is not completely rigid in the fresh condition, but presents a certain limited degree of flexibility. The body (Fig. 689) is star-shaped, consisting of a central part, the *central disc*, and five symmetrically arranged processes, the *arms* or *rays*, which, broad at the base, taper slightly towards their outer extremities. There are two surfaces—one, the *aboral* or *abactinal*, directed upwards in the natural position of the living animal; the other, the *oral* or *actinal*, directed downwards. The aboral surface is convex, the oral flat; the colour of the former is much darker than that of the latter.

In the centre of the oral surface (Fig. 689) is a five-rayed aperture, the *actinostome*, and running out from this in a radiating manner are five narrow grooves, the *ambulacral grooves*, each extending along the middle of the oral

surface of one of the arms to its extremity. Bordering each of the ambulacral grooves there are either two or three rows of movable calcareous spines, the *ambulacral spines*. At the central ends of the grooves the ambulacral spines of contiguous sides of adjacent grooves form five groups, the *mouth papillæ*, one at each angle of the mouth. External to the ambulacral spines are three rows of stout spines which are not movable; and a third series runs along the border separating the oral from the aboral surface.

On the convex aboral surface there are a number of short stout spines arranged in irregular rows parallel with the long axes of the rays. These are supported on irregularly-shaped ossicles buried in the integument. In the soft interspaces between the ossicles are a number of minute pores, the *dermal pores*, scarcely visible without the aid of a lens. Through each of these pores projects a very small, soft, filiform process, one of the *dermal branchiæ* or *papulæ* (Fig. 692, *Resp. cæ.*), which is capable of being entirely retracted.

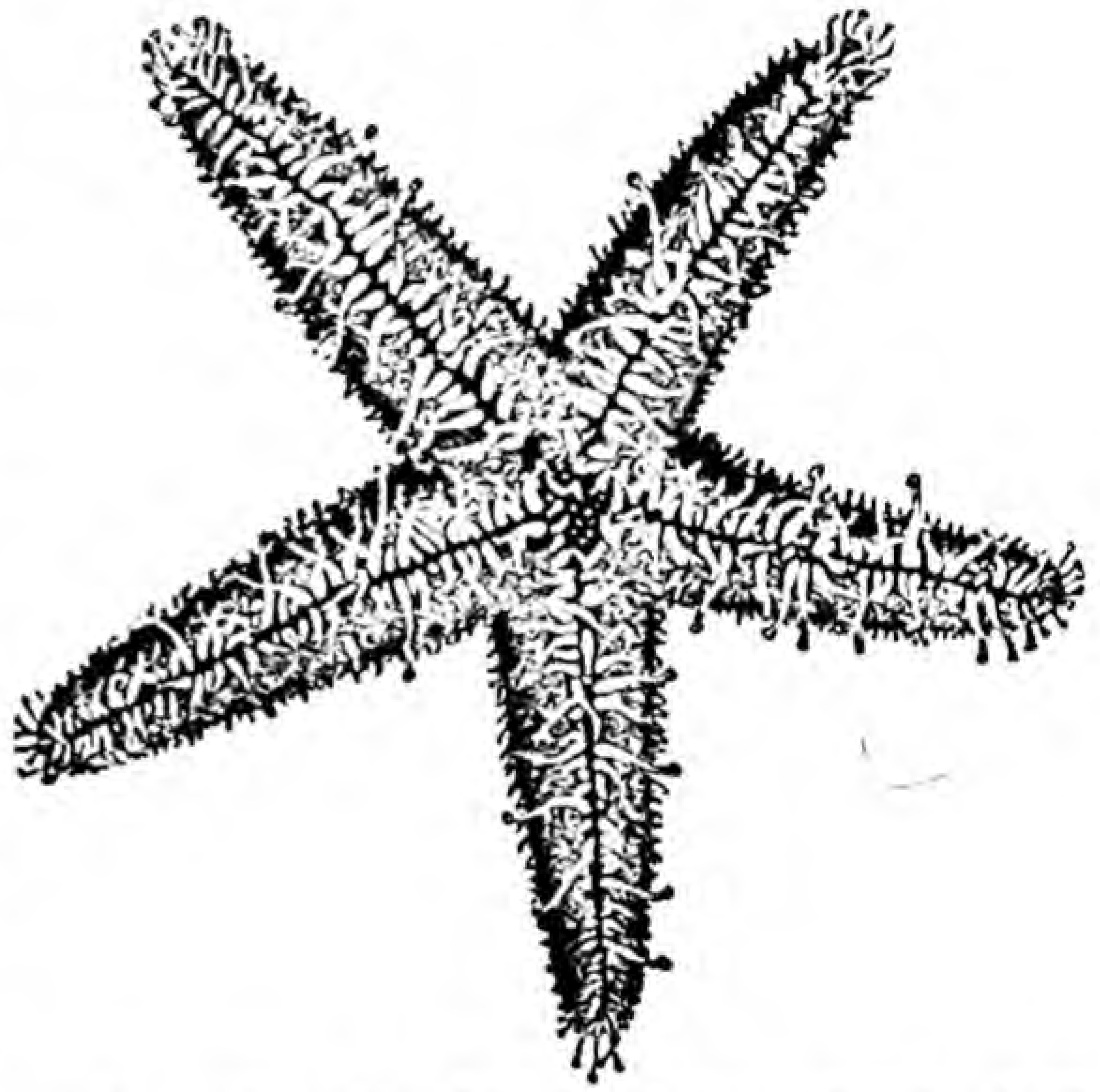


FIG. 689.—**Starfish** (*Asterias rubens*). General view of the oral or actinal surface, showing the tube-feet. (From Leuckart and Nitsche's Diagrams.)

Very nearly, though not quite, in the centre of the aboral surface is an aperture, the *anus* (Fig. 697), wide enough to admit of the passage of a moderately stout pin. On the same surface, midway between the bases of two of the rays, is a flat, nearly circular plate, the surface of which is marked by a number of radiating, narrow, straight, or slightly wavy grooves; this is the *madreporite* (*mad.*). The presence of this structure interferes to some extent with the radial symmetry of the Starfish, two of the antimeres, viz., those between which the madreporite is placed, being different from the rest. There thus arises a *bilateral* symmetry, there being one vertical plane, and only one—that passing through the middle of the madreporite and through the middle of the opposite arm—along which it is possible to divide the Starfish into two equal—right and left—portions.[1] The two rays between which the madreporite lies are termed the *bivium*, the three remaining the *trivium*.

Attached to the spines of the oral surface, in the intervals between them, and in the intervals between the spines of the dorsal surface, are a number of

[1] The slightly eccentric position of the anal aperture introduces a correspondingly slight inequality between the right and left portions.

very small, almost microscopic bodies, which are termed the *pedicellariæ* (Fig. 692, *Ped.*). Each of these is supported on a longer or shorter flexible stalk, and consists of three calcareous pieces—a *basilar* piece at the extremity of the stalk, and two *jaws*, which are movably articulated with the basilar piece, and are capable of being moved by certain sets of muscular fibres so as to open and close on one another like the jaws of a bird. In some of the pedicellariæ the jaws, when closed, meet throughout their entire length, while in the case of others, mostly arranged in circles round the spines on the aboral surface, one jaw crosses the other at the end like the mandibles of a Crossbill. Such pedicellariæ, with three calcareous pieces, are termed *forcipulate.*

In a well-preserved specimen there will be seen in each of the ambulacral grooves two double rows of soft tubular bodies ending in sucker-like extremities; these are the *tube-feet* or *podia* (Fig. 689). In a living specimen they are found to act as the locomotive organs of the animal. They are capable of being greatly extended, and when the Starfish is moving along, it will be observed to do so by the tube-feet being extended outwards and forwards (*i.e.*, in the direction in which the animal is moving), their extremities becoming fixed by the suckers, and then the whole tube-foot contracting so as to draw the body forwards; the hold of the sucker then becomes relaxed, the tube-foot is stretched forwards again, and so on. The action of all the tube-feet, extending and contracting in this way, results in the steady progress of the Starfish over the surface. With the aid of the tube-feet the Starfish is also able to right itself if it is turned over on its back.

At the extremity of each of the ambulacral grooves is to be distinguished a small bright red speck, the *eye* (Fig. 692, *A*, *oc.*), over which is a median process, the *tentacle* (*t.*), similar to the tube-feet, but smaller and without the terminal sucker. The tentacles have been ascertained by experiment to be olfactory organs, the Starfish being guided to its food much more by this means than by the sense of sight.

Transverse Section of an Arm.—If one of the arms be cut across transversely (Fig. 690 and Fig. 692, *B*) and the cut surface examined, the aboral part of the thick, hard wall of the arm will present the appearance of an arch (with its convexity upwards), and the oral part the form of a Λ, the ends of the limbs of which are connected with the oral ends of the aboral arch by a very short, flat, horizontal portion. Enclosed by these parts is a space, a part of the *cœlome* or *body-cavity*, and below, between the two limbs of the Λ is the ambulacral groove. The aboral arch is supported by a number of irregular ossicles and is perforated by the numerous small dermal pores, through which the dermal branchiæ project. The Λ-shaped oral part of the body-wall —*i.e.*, the walls of the ambulacral groove—is supported by two rows of elongated ossicles, the *ambulacral ossicles* (Fig. 692, *Amb. os.*), which meet together at the apex or summit of the groove like the rafters supporting the roof of a house,

but with a movable articulation allowing of separation or approximation of the two rows so as to open or close the groove. At the end of the ray the ambulacral ossicles end in a median *terminal* ossicle. At the edges of the groove a row of ossicles support the ambulacral spines and prominent tubercles. Between the ambulacral ossicles of each row are a series of oval openings, the *ambulacral pores*, one between each pair of contiguous ossicles, and so arranged that they form two rows on each side, one row higher than the other, the pores of the higher row alternating with those of the lower. In the ventral groove lie the contracted tube-feet (*T. F.*) : each tube-foot is found to correspond to one of the ambulacral pores, so that the former, like the latter, are arranged in a double alternating row on each side of the groove. When the tube-foot is drawn upon, it is seen to be continuous with one of a series of little bladder-like bodies, which lie on the other side of the ambulacral ossicles, *i.e.*, in the cavity of the arm. These —the *ampullæ* (Figs. 690 and 692, *amp.*)—are arranged like the tube-feet, in a double row on each side, a higher row and a lower, there being one opposite each ambulacral pore. When one of them is squeezed, the corresponding tube-foot is distended and protruded, the cavities of the tube-foot and ampulla being in communication by means of a narrow canal running through the ambulacral pore and provided with a valve. It is in this way that the foot is protruded in the living animal: the corresponding ampulla being contracted by the contraction of the muscular fibres in its walls, the contained fluid is injected into the tube-foot and causes its protrusion, the return of the water backwards through the canal being prevented by the closing of the valve.

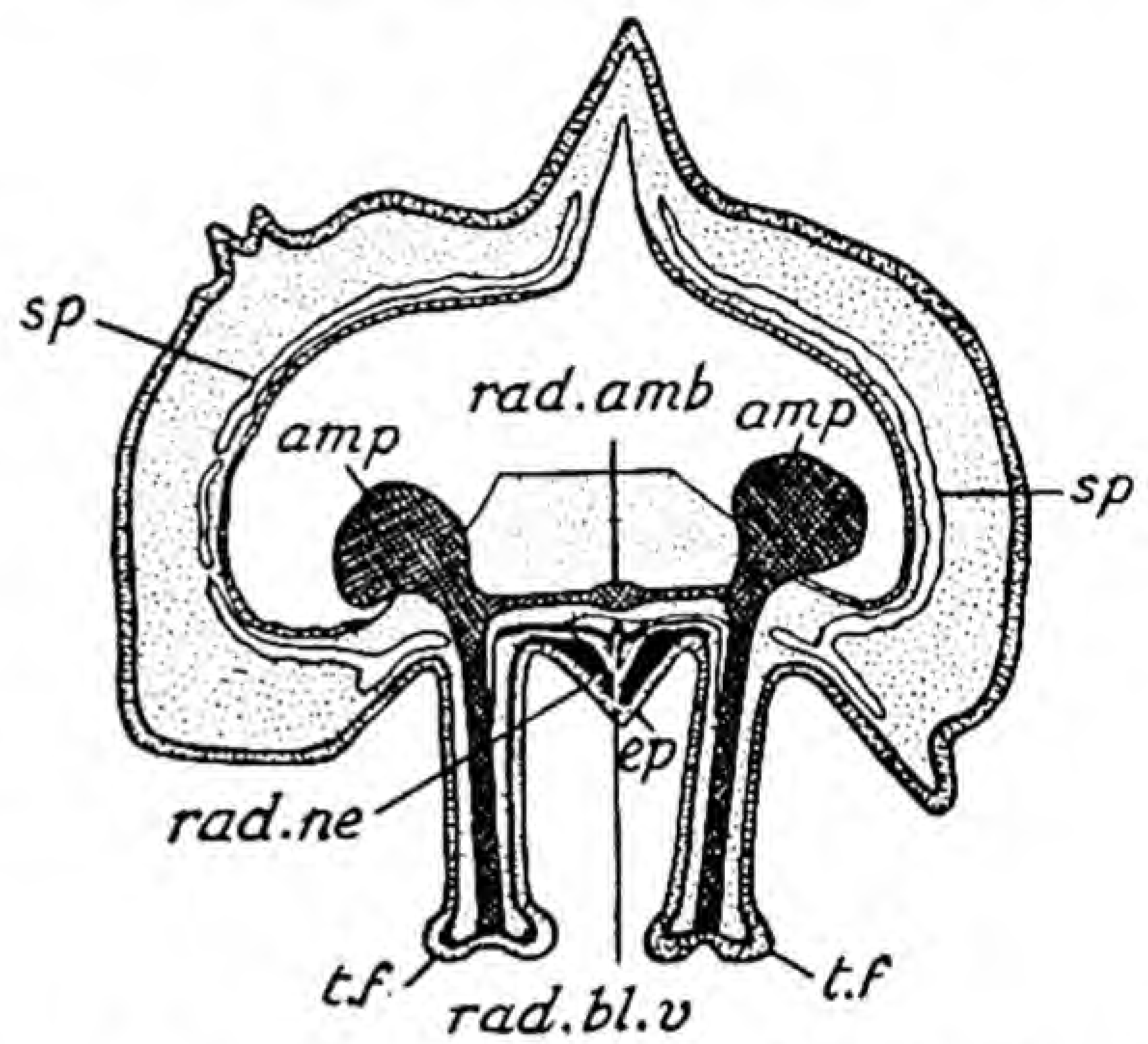


FIG. 690.—**Starfish.** Vertical section through an arm. *amp.* ampullæ; *ep.* epidermis; *rad. amb.* radial vessel of the ambulacral system; *rad. bl. v.* points to the septum dividing the perihæmal vessel into two parts; *rad. ne.* radial nerve of the epidermal system; *sp.* spaces in mesoderm of body-wall; *t. f.* tube-feet. (From Leuckart, after Hamann.)

Vascular and Nervous Systems.—Running along the ambulacral groove, immediately below where the ambulacral ossicles of opposite sides articulate, is a fine tube, the *radial ambulacral vessel* (Fig. 690, *rad. amb.*), which appears in the transverse section as a small rounded aperture. From this short side-branches pass out on either side to open into the bases of the tube-feet. Below the radial ambulacral vessel is a median thickening of the integument covering the ambulacral groove : this marks the position of the *radial nerve* (Fig. 690,

rad. ne.) of the *epidermal nervous system*, and is traceable as a narrow thickened band running throughout the length of the groove, and terminating in the eye at its extremity, while internally it becomes continuous with one of the angles of a pentagonal thickening of a similar character, the *nerve-pentagon*, which surrounds the mouth. In thin sections (Fig. 691) the ventral median thickening, or *radial nerve* (*rad. nerv.*), as well as the nerve-pentagon, are seen to be thickenings of the epidermis, consisting of numerous vertically-placed, fibre-like cells, with their nuclei at their outer (lower) ends, intermixed with longitudinal nerve-fibres and with nerve-cells. Above this, on each side of the epidermal nerve-thickening constituting the radial nerve, is a band of cells (*d. nerv.*) also of a nervous character. These more deeply placed nerve-bands are the radial parts of the *deep nervous system*: like the epidermal, the deep nervous system has a central part in the form of a pentagon, which in this case is double, surrounding the mouth. A third set of nerve elements (the *aboral* or *cœlomic nervous system*) extends along the roof of the arm superficial to the muscles.

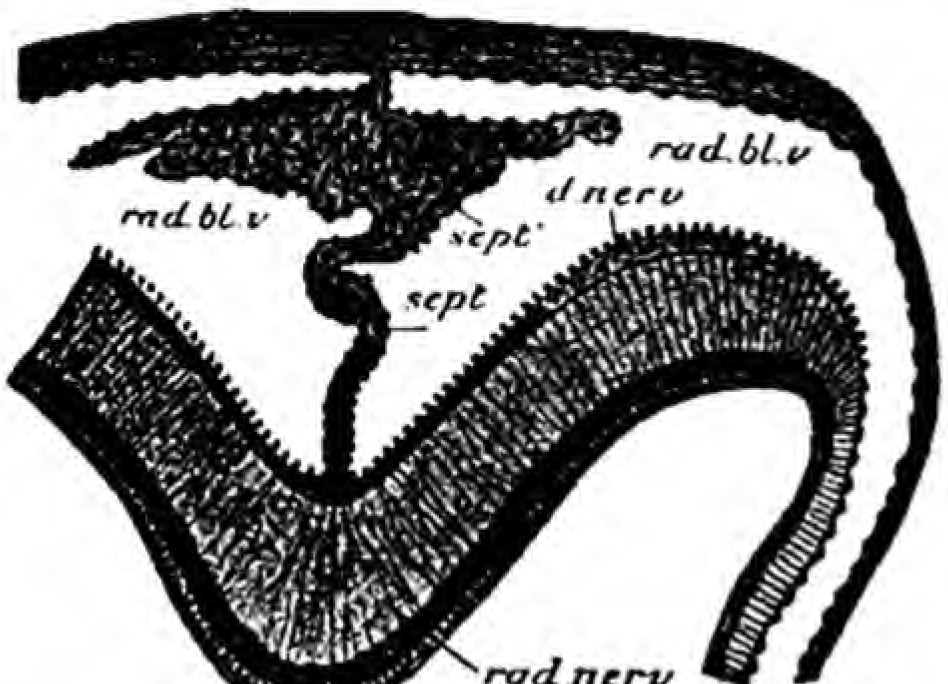


FIG. 691.—**Starfish.** Lower part of a vertical section through the arm, to show the structure of the radial nerve and the position of the deep nervous system and radial perihæmal vessels. *d. nerv.* strand of deep nervous system; *rad. bl. v.* radial perihæmal vessel; *rad. nerv.* radial nerve; *sept.* septum of radial perihæmal vessel; *sept'.* radial lacunar strand of the hæmal system (here represented as solid). (After Cuénot.)

The two radial nerve-bands of the deep nervous system are thickenings of the lining membrane of a space overlying the radial nerve and underlying the radial ambulacral system. This space (*rad. bl. v.*), extending, like the other parts that have been mentioned, throughout the length of the arm, forms part of a system of channels, the *perihæmal system*, which have been regarded as constituting a blood-vascular system. This *radial perihæmal vessel* or *sinus*, as it is termed, is divided longitudinally by a vertical septum (*sept.*) into two lateral halves. Internally it communicates with an *oral ring-vessel* surrounding the mouth and likewise divided into two by a septum. The inner division of the ring-vessel is connected with the *axial sinus* referred to on p. 696.

In the septum dividing the radial perihæmal sinus into two runs a strand of a kind of gelatinous connective tissue containing many leucocytes and perforated by irregular channels or *lacunæ*: this is the radial strand of the *lacunar* or *hæmal system*. Like the radial vessels of the perihæmal system, the radial strands of the lacunar system are connected internally with an oral ring.

Structure of the Disc.—When the aboral wall of the central disc is dissected away, the remainder of the organs come into view (see Fig. 695). The rows of ambulacral ossicles appear in this view as ridges, the *ambulacral ridges*, one

running along the middle of the oral surface of each arm to its extremity, and extending inwards to the corresponding angle of the mouth. At the sides of each of these ridges appear the rows of ampullæ. Within the pentagonal actinostome is a space, the *peristome*, covered with a soft integument, and in the

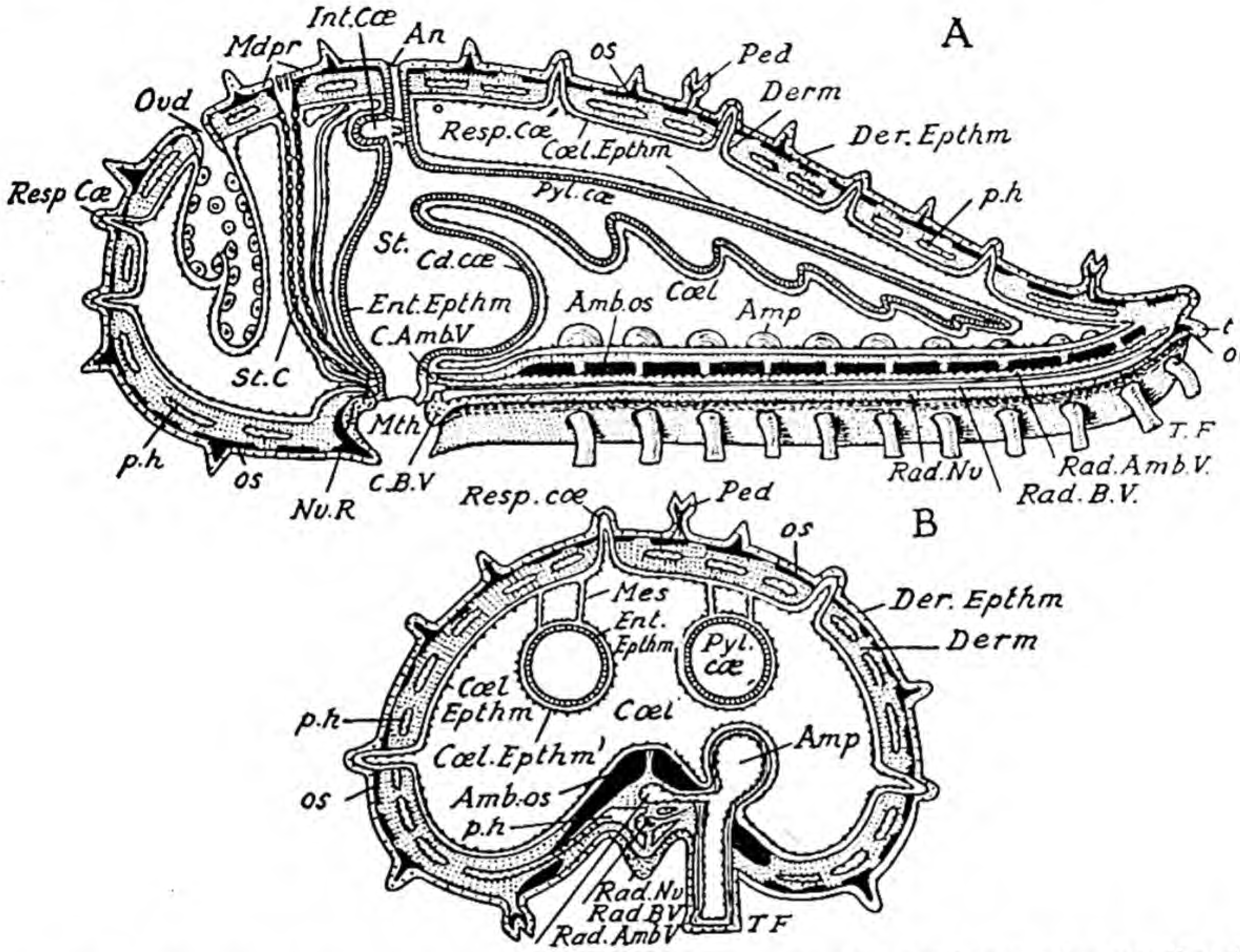


FIG. 692.—Diagrammatic sections of a **Starfish.** *A*, vertical section passing on the right through a radius, on the left through an inter-radius. The off-side of the ambulacral groove with the tube-feet (*T. F.*) and ampullæ (*Amp.*) are shown in perspective. *B*, transverse section through an arm. The ectoderm is coarsely dotted, the nervous system finely dotted, the endoderm radially striated, the mesoderm evenly shaded, the ossicles of the skeleton black, and the cœlomic epithelium represented by a beaded line. *Amb. os.* ambulacral ossicles; *Amp.* ampullæ; *An.* anus; *C. Amb. V.* circular ambulacral vessel; *C. B. V.* septum of ring perihæmal vessel; *Cd. cœ.* cardiac cæca; *Cœl.* cœlome; *Cœl. Epthm.* cœlomic epithelium; *Der. Epthm.* deric epithelium; *Derm.* mesoderm; *Ent. Epthm.* enteric epithelium; *Int. cœ.* intestinal cæca. *Mdpr.* madreporite; *Mes.* mesentery; *Mth.* mouth; *Nv. R.* nerve-ring; *oc.* eye; *os.* ossicles of body-wall; *Ovd.* oviduct; *Ped.* pedicellariæ; *p. h.* perihæmal spaces; *Pyl. cœc.* pyloric cæca; *Rad. amb. v.* radial ambulacral vessel; *Rad. B. V.* points to septum in the radial perihæmal vessel; *Rad. Nv.* radial nerve; *Resp. cœ.* dermal branchiæ; *St.* stomach; *St. c.* stone-canal; *t.* tentacle; *T. F.* tube-feet. (From Parker's *Biology*.)

centre of this is a circular opening, the true *mouth*, the size of which is capable of being greatly increased or diminished.

Body-wall and Cœlome.—The entire outer surface is covered with a layer of ciliated epithelium, the *epidermis* or *deric epithelium* (Fig. 692, *Der. Epthm.*),

which is continued over the various appendages and processes—the tubercles and spines, the pedicellariæ, the dermal branchiæ, and the tube-feet. Beneath it is a network of nerve-fibrils with occasional nerve-cells. The *mesoderm* (*Derm.*) of the wall of the body beneath this consists of two layers, between which are a number of spaces: the ossicles (*os.*) are all, except the ambulacral ossicles and the inter-radial partitions, developed in the outer of these two layers. Each *ossicle* consists of a close network of calcareous rods. Between contiguous ossicles extend bands of muscular fibres.

The interior of the *cœlome* (*Cœl.*) or body-cavity is lined by a ciliated epithelium, the *cœlomic epithelium* (*Cœl. Epthm.*), which not only covers the inner surface of the body-wall as the *parietal layer*, but also forms an investment for the contained organs—the various parts of the alimentary canal and its appendages, the gonads, the madreporic canal, ampullæ, etc. In addition to this *visceral layer* of the peritoneum, the wall of the alimentary canal and its cæca consists of a *muscular layer* and an internal lining, the *enteric epithelium* or *endoderm* (*Ent. Epthm.*). The cœlome is filled with a fluid, the *cœlomic fluid*, similar in composition to sea-water, but containing a number of amœboid corpuscles (*amœbocytes*). These collect particles of waste-matters, and when loaded with them pass to the exterior by traversing the walls of the papulæ. The latter consist of a *muscular layer*, an *external epidermal layer*, and an *internal peritoneal layer*, the internal cavities being in free communication with the cœlome.

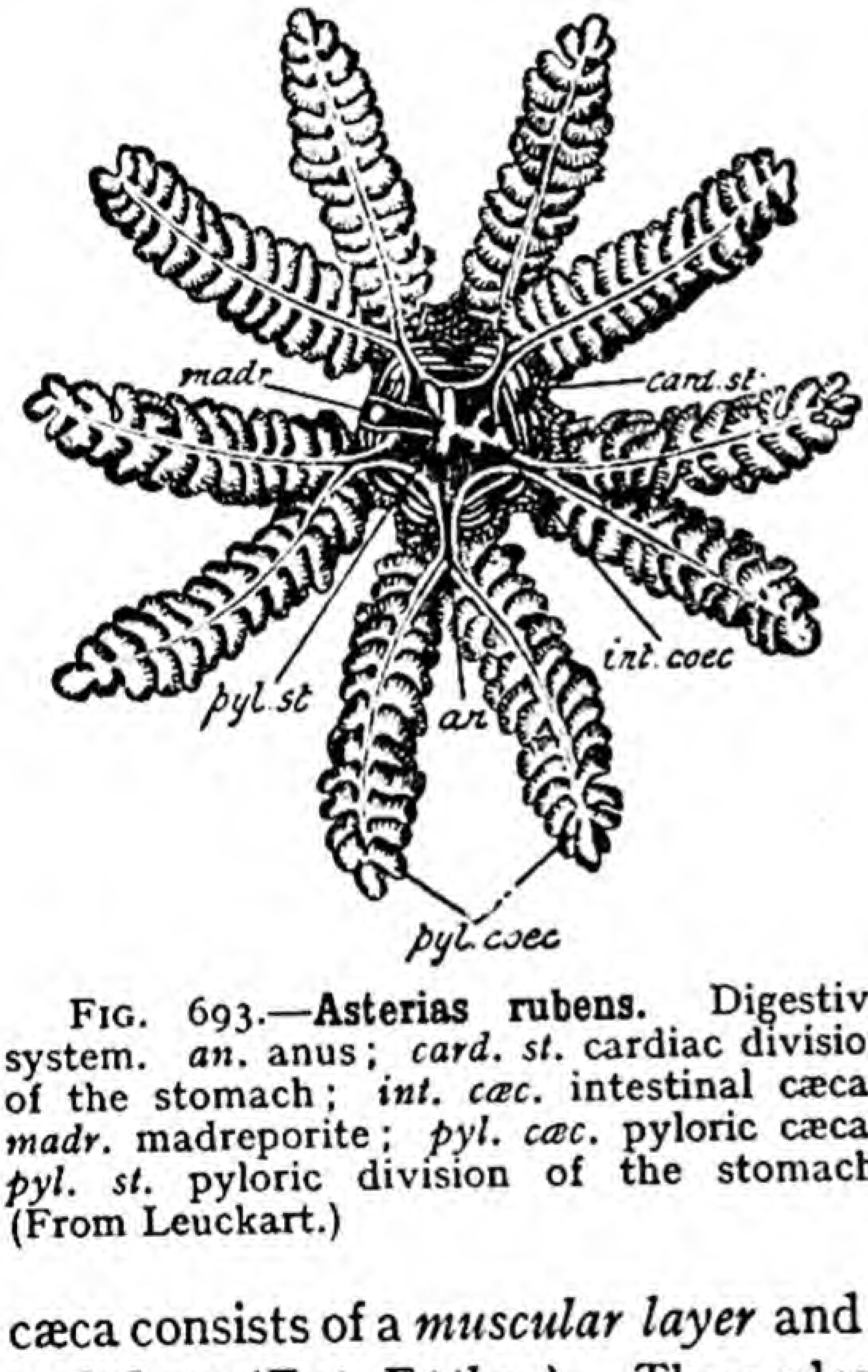


FIG. 693.—**Asterias rubens.** Digestive system. *an.* anus; *card. st.* cardiac division of the stomach; *int. cæc.* intestinal cæca; *madr.* madreporite; *pyl. cæc.* pyloric cæca; *pyl. st.* pyloric division of the stomach. (From Leuckart.)

FIG. 694.—Transverse section through the madreporic canal of a **Starfish** (*Astropecten*). (From Gegenbaur, after Teuscher.)

Digestive System.—The mouth is found to open through a short passage, the *œsophagus*, into a wide sac, the *cardiac division of the stomach* (Fig. 692, *St.*, Figs. 695, 697, *card. st.*). This is a five-lobed sac, each of the lobes of which is opposite one of the five arms. The walls of the sac are greatly folded, and

the whole is capable of being everted through the opening of the mouth, by contraction of the muscular fibres of the body-wall, wrapped over some object desired as food, and then retracted into the interior, the retraction being effected by means of special *retractor* muscles (Fig. 695, *retr.*) which arise from the sides of the ambulacral ridges. This cardiac division of the stomach com-

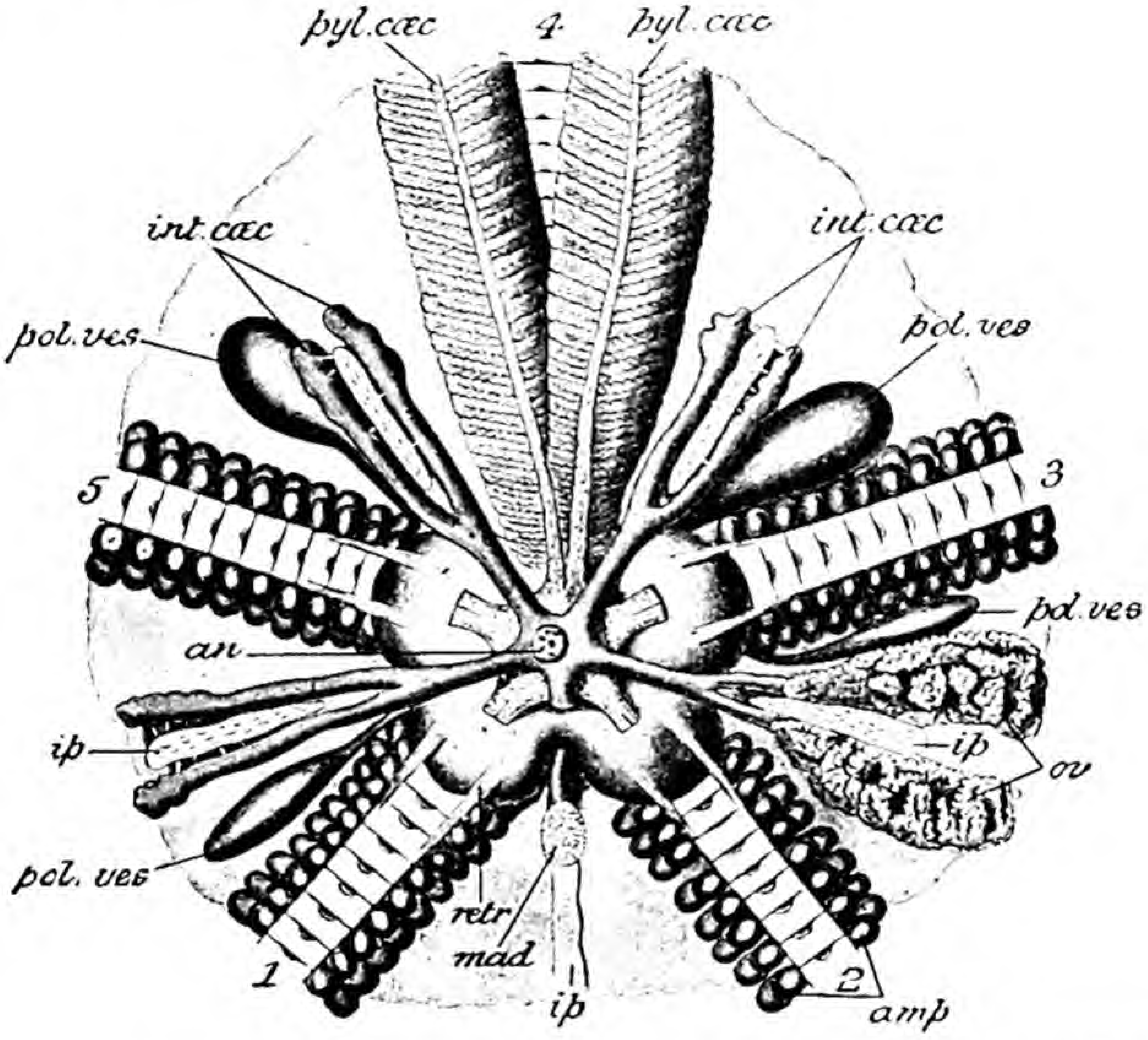


FIG. 695.—**Anthenea flavescens.** Upper view of a dissection of the internal organs. The aboral wall of the body, with the exception of a small portion round the anus and the madreporite, has been completely removed. One of the five intestinal cæca has been removed with the exception of its proximal part. All the ovaries have been removed except one pair, and four of the pairs of pyloric cæca have been cut away close to their bases. 1—5, the five rays with their ambulacral ridges; *amp.* ampullæ; *an.* anus; *int. cæc.* intestinal cæca; *i. p.* cut ends of the inter-radial partitions; *mad.* madreporite with the madreporic canal; *ov.* ovaries; *pol. ves.* Polian vesicles; *pyl. cæc.* pyloric cæca; *retr.* retractor muscles inserted into the cardiac division of the stomach.

municates aborally with a much smaller chamber, the *pyloric division of the stomach*, and this in turn opens into a very short conical *intestine*, which leads directly upwards to open at the anal aperture. The pyloric division of the stomach is pentagonal, each angle being drawn out to form a pair of large appendages, the *pyloric cæca* (Figs. 692, 693, 694, 695, *pyl. cæc.*). Each pair of pyloric cæca commences as a cylindrical canal or *duct*, the lumen of which is continuous with the cavity of the pyloric chamber. This soon bifurcates to

form two hollow stems, extending to near the extremity of the cavity of the arm, and giving off laterally two series of short branches, each having connected with it a number of small bladder-like pouches. The walls of the pyloric cæca are glandular: they secrete a digestive fluid, and are therefore to be looked upon as *digestive glands.* It is found by experimenting with this digestive fluid that it has an action on food-matters similar to that exerted

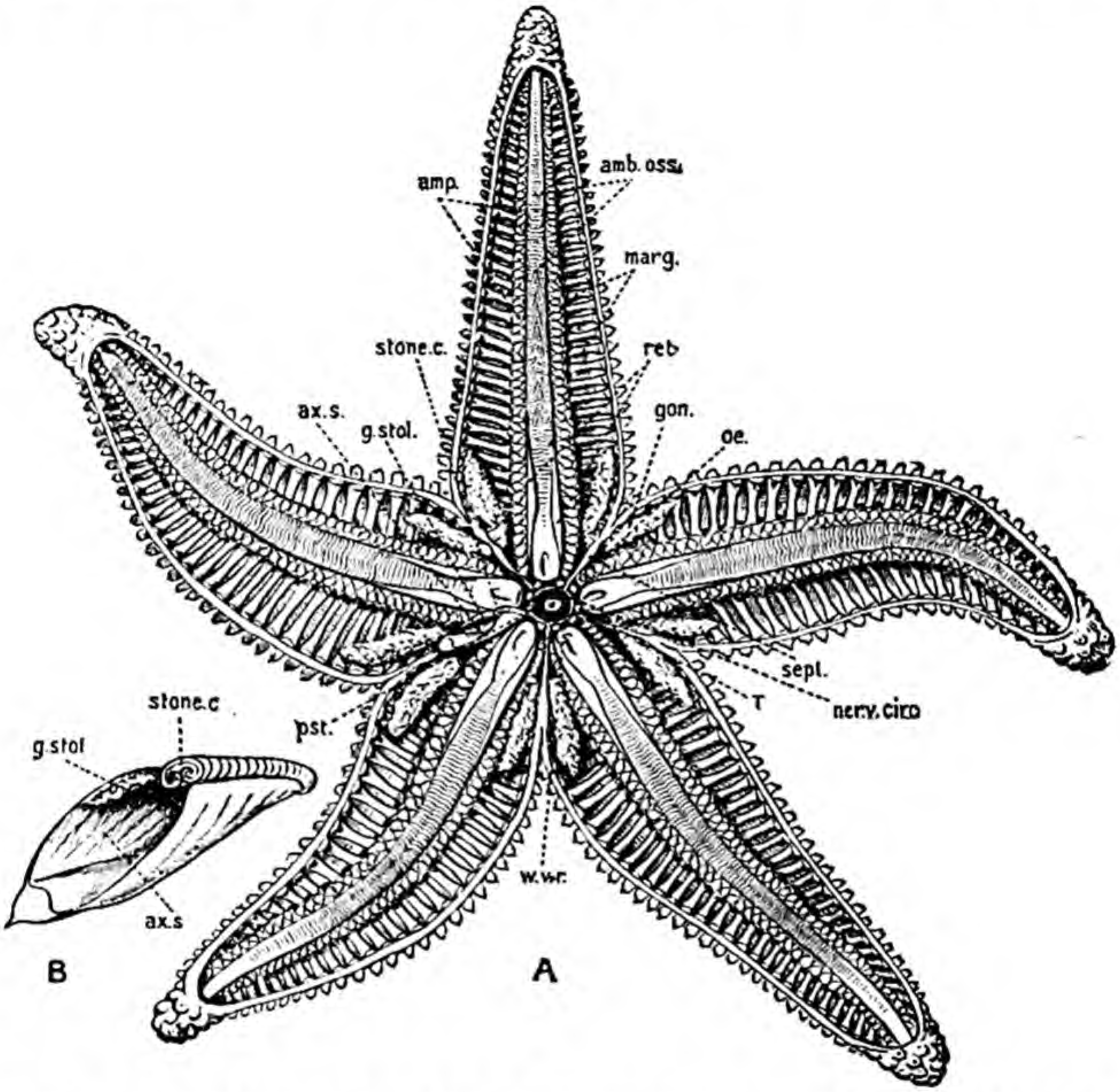


FIG. 696.—*A*, view of the under part of a specimen of **Asterias rubens**, which has been horizontally divided into two nearly equal portions. *B*, enlarged view of the axial sinus, stone-canal and genital stolon cut across. *amb. oss.* ambulacral ossicle; *amp.* ampullæ of the tube-feet; *ax. s.* axial sinus; *gon.* gonad; *g. stol.* genital stolon or axial organ; *marg.* marginal ossicle; *nerv. circ.* nerve-ring; *oe.* cut end of œsophagus; *pst.* peristome; *ret.* retractor muscle of the stomach; *sept.* inter-radial septum; *stone. c.* stone-canal; *T.* Tiedemann's vesicle; *w. v. r.* water-vascular ring-canal. (After MacBride.)

by the secretion of the pancreas in the Vertebrata containing enzymes for the digestion of carbohydrates, proteins, and fat. While the pouches of the cardiac division of the stomach are attached to the oral wall of the body, the pyloric cæca are connected with the aboral wall. From the short intestine are given off inter-radially two hollow appendages, the *intestinal cæca* (Figs. 693 and 695, *int. cæc.*), each with several short branches of irregular shape.

Ambulacral System.—Running downwards from the madreporite to near

the border of the mouth is an S-shaped cylinder, the *madreporic* or *stone-canal* (Fig. 697, *mad. can.*). The walls of this canal are supported by a series of calcareous rings, and projecting into it is a ridge which bifurcates to form two spirally rolled lamellæ occupying a considerable part of the lumen of the canal. In some Starfishes, such as Astropecten (Fig. 694), the internal structure is more complicated owing to the branching of the lamellæ. The interior of the madreporic canal communicates above with the exterior through the grooves of the madreporite. At the bottom of each of the grooves are a number of fine pores leading into vertical canals of corresponding fineness, all lined, like the grooves and the madreporic canal itself, with long cilia: most of these open below into a dilatation of the madreporic canal, some into the axial sinus

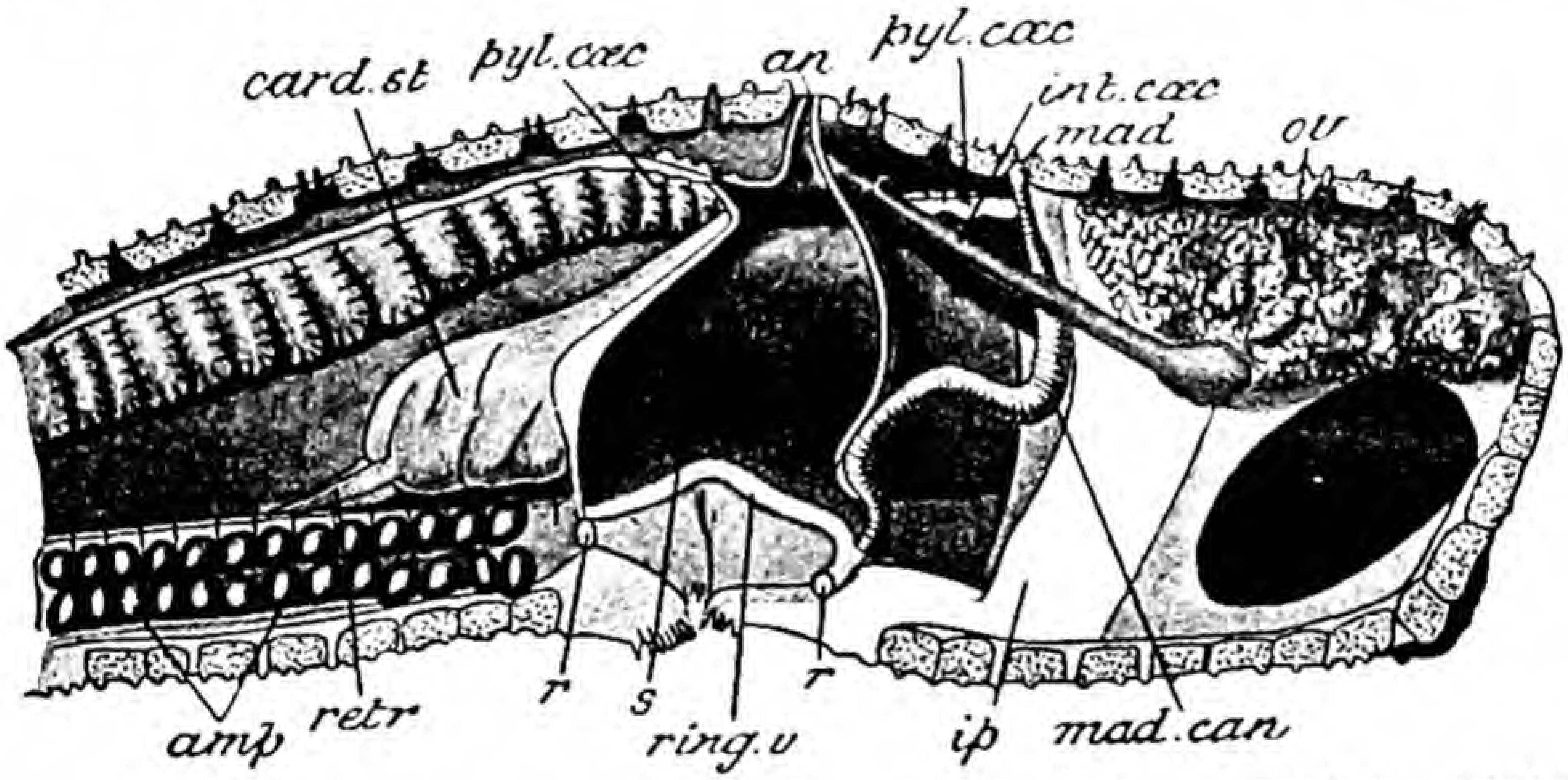


FIG. 697.—**Anthenea flavescens.** Lateral view of a dissection in which one of the rays and a portion of a second have been removed, and in which the alimentary canal has been laid open. *amp.* ampullæ; *an.* anus; *card. st.* cardiac pouch of the stomach; *int. cæc.* intestinal cæcum; *ip.* inter-radial partition; *mad.* madreporite; *mad. can.* madreporic canal; *ov.* ovary; *pyl. cæc.* pyloric cæca; *r.* cut ends of the ring-vessel of the ambulacral system; *ring. v.* position of the ring-vessel; *retr.* retractor muscle of cardiac pouch of stomach; *s.* cavity of the stomach.

referred to below. Below, the madreporic canal opens into a wide, five-sided, ring-like canal, the *ring-vessel of the ambulacral system*. From this are given off the five radial ambulacral vessels, passing to the extremities of the arms. From the pentagonal canal are given off also in most Starfishes, but not in Asterias, a series of five pairs of appendages, the *Polian vesicles* (Fig. 695, *pol. ves.*)—pear-shaped, thin-walled bladders with long narrow necks—which are placed inter-radially. At the sides of the neck of each Polian vesicle (except in the inter-radius containing the madreporic canal, where there is one on one side only) project inwards a pair of little rounded glandular bodies, the *racemose* or *Tiedemann's vesicles* (Fig. 696, *T.*), the cavity in the interior of each of which, opening into the ring-vessel, is divided into a number of chambers.

The various parts of the ambulacral system of vessels have a muscular wall and an internal lining epithelium in addition to the coverings which they

may derive, according to their situation, either from the external epidermis or the internal cœlomic epithelium. The muscular layer is most strongly developed on the tube-feet, where it consists of two strata, and is also well developed on the ampullæ and Polian vesicles.

The stone-canal is enfolded in the wall of a wider canal, the *axial sinus* (Fig. 696, *ax. s.*, and Fig. 698), which forms a part of the perihæmal system already referred to. The axial sinus runs nearly vertically. At its oral end it opens into the internal division of the oral ring sinus; aborally it approaches

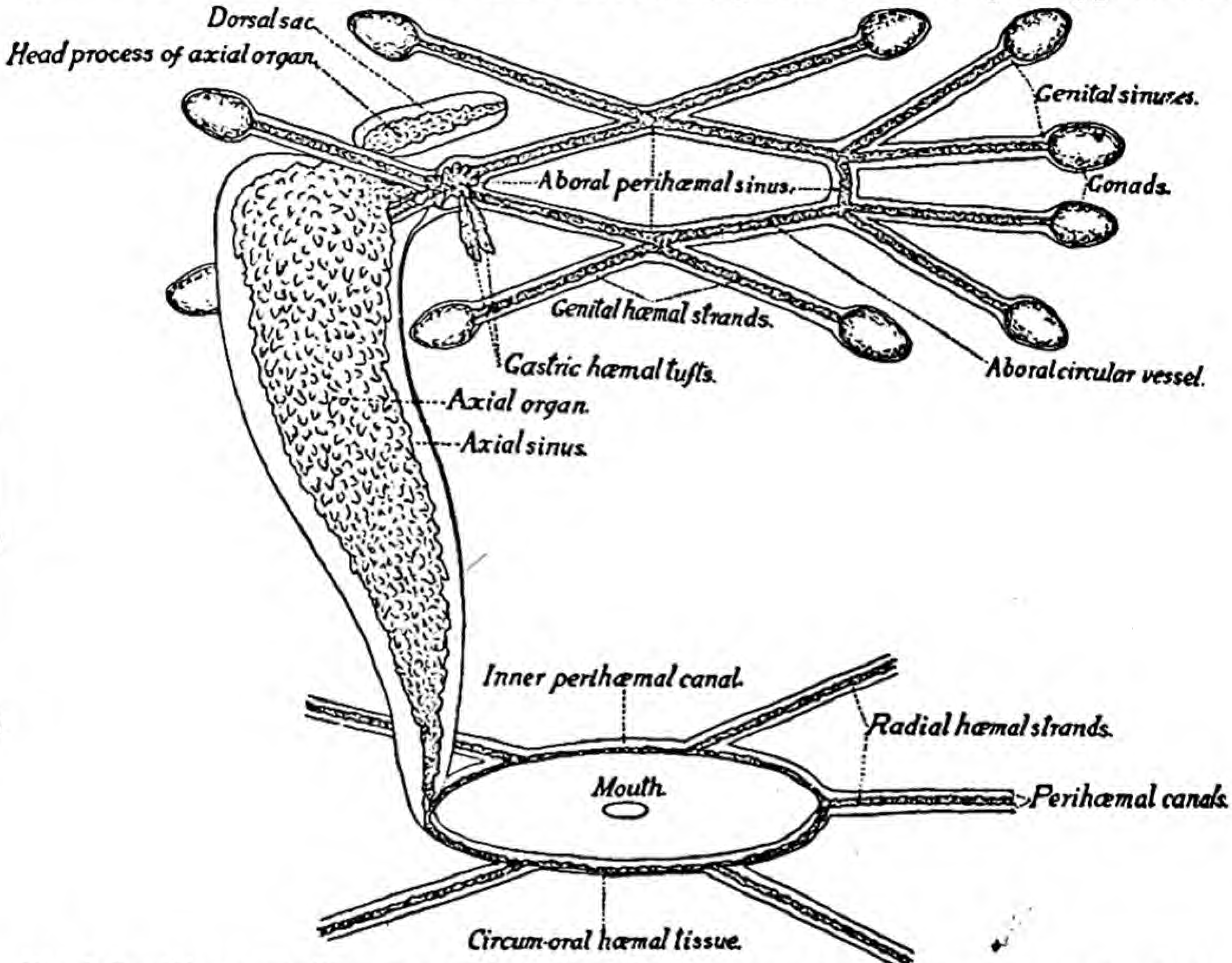


FIG. 698.—Diagram to illustrate the axial organ of **Asterias** and its relation to the oral and aboral circular hæmal strands of hæmal tissue proceeding therefrom; also the sinuses in which these structures are enclosed. (From Chadwick's *Asterias* (The Liverpool University Press, Ltd.).)

close to, if it does not actually open into, an *aboral ring sinus:* it also communicates aborally with the stone-canal, and opens on the exterior through certain of the pores in the madreporite.

Accompanying the madreporic canal and also enfolded in the wall of the axial sinus there is an organ—the *axial organ* (Fig. 696, *g. stol.*; Fig. 698)—the relationships and function of which have given rise to a considerable amount of difference of opinion. It is a fusiform body, the interior of which assumes an appearance of complexity largely due to both its inner surface (*i.e.*, that turned towards the axial sinus) and its outer (that facing the cœlome) being

folded in a complicated manner. The axial organ contains strands of lacunar tissue, *i.e.*, of the same tissue that composes the so-called hæmal system, and is intimately related with the latter. Its essential morphological character, however, appears to be that of a *genital stolon*. At its aboral end it is continuous with a *genital rachis*, which, in the form of a ring, runs in the aboral periphæmal sinus, and gives off branches to the gonads. There is evidence that the sexual cells originate in the aboral end of the axial organ, and travel through the genital rachis and its branches to the gonads, which are to be looked upon as the greatly expanded extremities of the latter. Strands of the lacunar tissue accompany the genital rachis and its branches to the gonads.

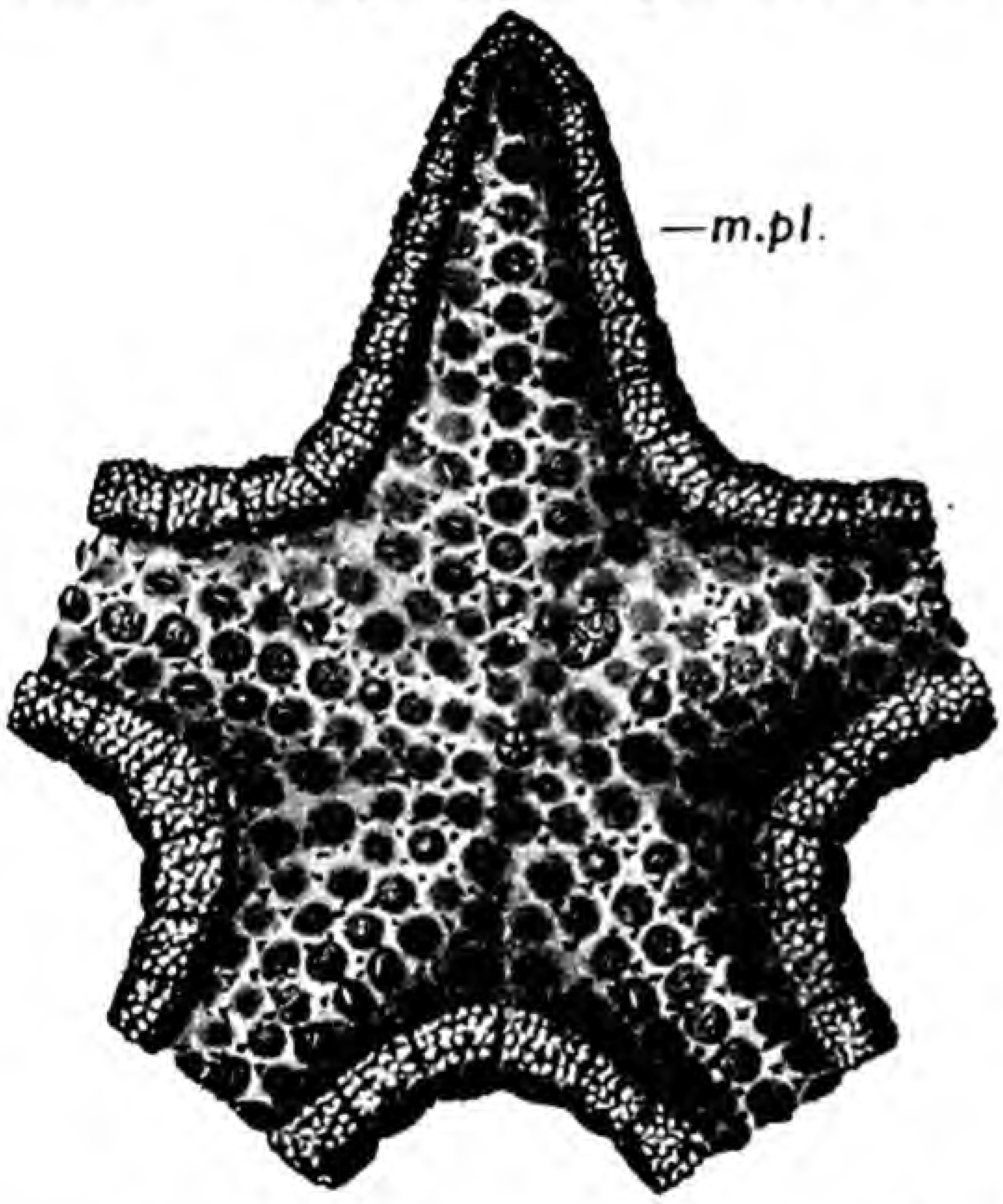


FIG. 699.—**Anthenea,** view of aboral surface showing granular ossicles, marginal plates (*m. pl.*), madreporite and anus. (After Sladen.)

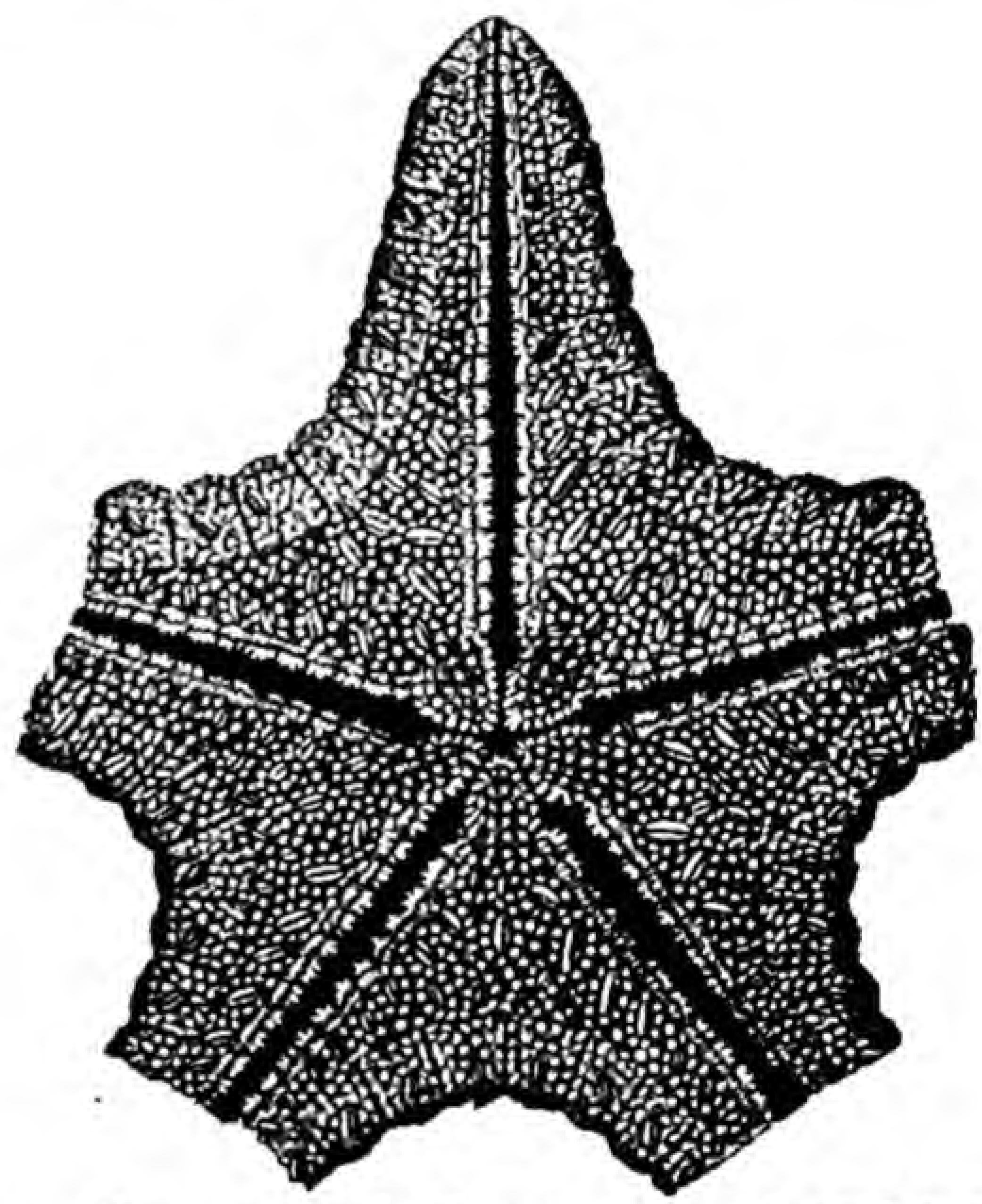


FIG. 700.—**Anthenea,** view of oral surface, showing ambulacral grooves with small ambulacral spines, mouth-papillæ and valvate pedicellariæ. (After Sladen.)

Reproductive System.—The Starfish is *unisexual*, each individual possessing either *ovaries* (Figs. 695, *ov.*, 696, *gon.*, and 697, *ov.*) or *testes*, which appear very similar until they are examined microscopically. They consist of masses of rounded follicles, like bunches of minute grapes—a pair in each inter-radial interval. Ova and sperms have been described to develop from cells of the same character as those which become the amœbocytes of the cœlomic and other cavities of the body. The ducts, by means of which the ova or sperms reach the exterior, open on the aboral surface through a number of perforations on a pair of sieve-like plates, situated inter-radially close to the bases of the arms.

Anthenea flavescens (Figs. 695, 697, 699, 700), a common Australian Starfish, which may be taken as an example instead of *Asterias rubens*, differs from the latter in the following main points.

The animal consists of a relatively large central disc and five relatively short arms, which taper rapidly towards their extremities. On the oral surface the comparatively broad, flat surfaces between the ambulacral grooves are roughish, owing to the plate-like ossicles being beset with a number of minute rounded *tubercles* or *granules*, which, in the immediate neighbourhood of the ambulacral grooves, assume the character of short, blunt spines. Here and there among the tubercles, usually one in the middle of each ossicle, are *pedicellariæ*, which differ widely from those of Asterias. Each pedicellaria in Anthenea is a small, narrow, oblong, calcareous body, consisting of two parallel narrow valves or jaws: these, instead of being supported on a flexible stalk, are articulated with the edges of a slit-like depression on the surface of the flat ossicle, and are thus on a level with the general surface. The term *valvate* is applied to pedicellariæ of this description. In a living *Anthenea* many of the pedicellariæ will be found to have their valves widely open; when they are touched the valves close together, gradually opening again after a little time. The *ambulacral spines* bounding the ambulacral grooves are flattened and blunt, and arranged in fan-like fasciculi. Round the border separating the aboral and oral surfaces the plates are arranged in two somewhat irregular rows.

The aboral surface is strongly convex, but not uniformly so, there being a more or less distinct depression in the form of a shallow open groove, the *inter-radial depression*, opposite each of the intervals between the arms. The surface is dotted over with numerous small rounded *tubercles*, arranged in somewhat irregular radiating lines. These aboral tubercles, though fewer than those in the oral surface, are for the most part more prominent, so that they assume the character of short spines. The ossicles on which they are borne are star-shaped with six rays, a spine being borne in the centre of each ossicle, and one on each of the rays. Between the ossicles the surface is covered with a soft, slimy skin, perforated by a large number of minute dermal pores, each of which is enclosed by a minute irregular ring of calcareous matter; each pore serves for the lodgment of one of the dermal branchiæ. Numerous pedicellariæ, similar to those on the ventral surface, but smaller, are borne on the ossicles, usually taking the place normally occupied by the central spine. The *tube-feet* are arranged in a single row on each side of each ambulacral groove; but the *ampullæ* are in two rows, an upper and a lower, and each tube-foot has two ampullæ connected with it, one of the upper row and one of the lower row.

Anthenea has vertical calcareous *inter-radial partitions* not developed in Asterias. There are five bifid *intestinal cæca*, which are narrow tubes, slightly enlarged and lobed at the extremities.

Development of a Starfish (Asterina gibbosa or A. exigua).[1]—In these Starfishes the reproductive apertures are placed on the ventral surface. When

[1] The development of these has been described in preference to that of the examples as it is more completely known.

the ova have been discharged and fertilized, they adhere by means of a viscid investment to the surface (rock or stone) on which they are laid, and go through all the stages of their development in this position, never passing through a free pelagic stage. The eggs are about half a millimetre in diameter, and of a spherical shape. Each consists of a perfectly opaque central mass of yellow or orange yolk, and of a glassy layer enclosing this. After fertilization the process of cleavage begins by the division of the ovum into two blastomeres almost equal in size, but one, which may be termed cell I., slightly smaller than the other (cell II.). Both I. and II. soon afterwards divide, I. somewhat earlier than II. The resulting four cells again divide, leading to the formation of an eight-celled stage (Fig. 701, *A*), in which the four cells derived from I.

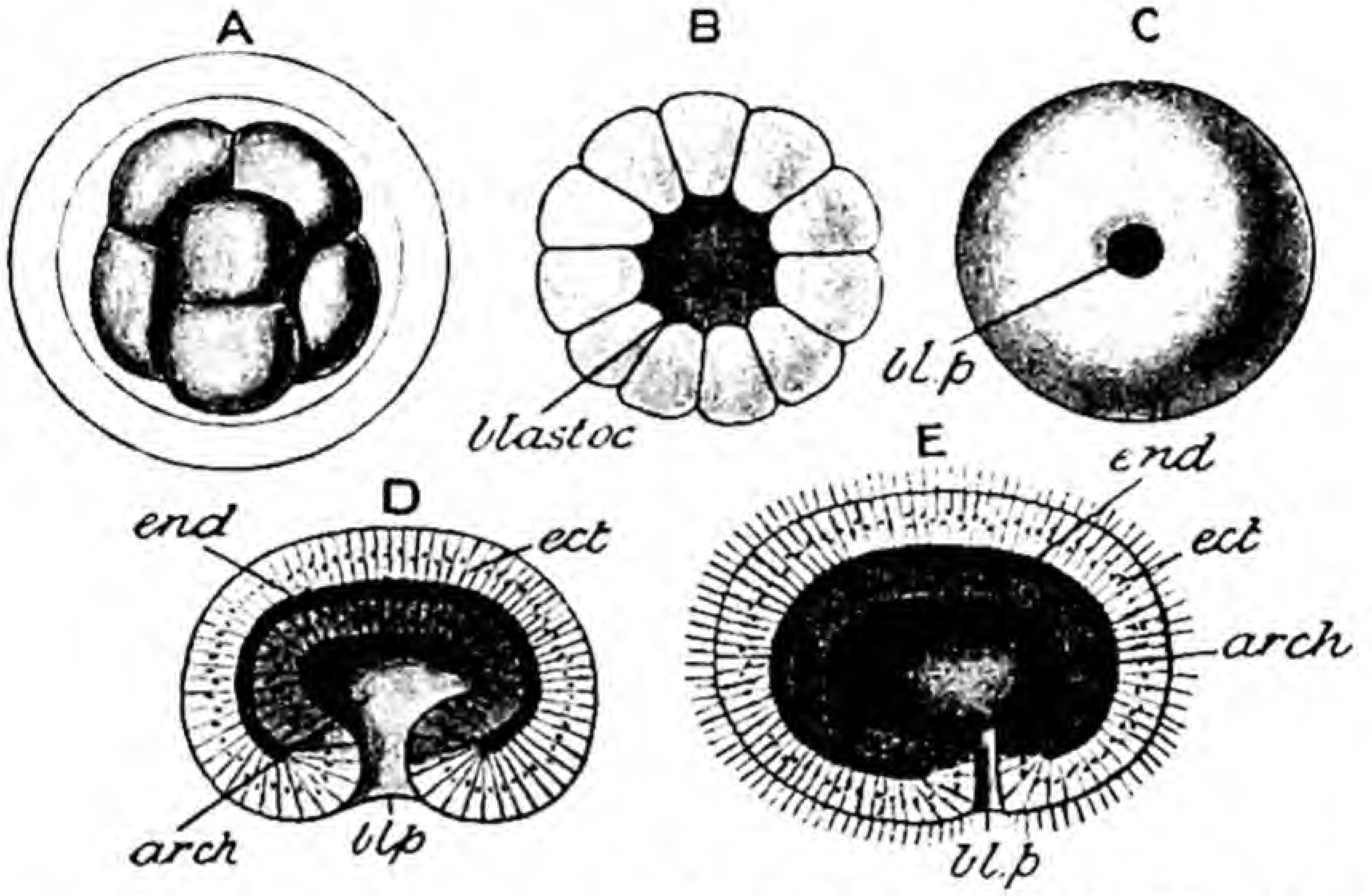


FIG. 701.—Early stages in the development of a Starfish (**Asterina gibbosa**). *A*, eight-celled stage; *B*, stage of about thirty-two cells seen in section; *C*, gastrula stage; *D*, section of early gastrula; *E*, section of later gastrula. *arch.* archenteron; *blastoc.* blastocœle; *blp.* blastopore: *ect.* ectoderm; *end.* endoderm. (Modified after Ludwig.)

form an incomplete ring not closed below, and the four derived from II. form an incomplete ring open above.

The eight cells then divide by meridional fissures into sixteen, and a further division results in the formation of thirty-two. The thirty-two cells become arranged in such a way as to enclose a central cavity which had been present in the four-celled stage: this stage (*B*) is the *blastula*; the cavity is the *blastocœle.* The number of cells in the wall of this cavity increases by further divisions, and the whole surface becomes covered with vibratile cilia. A process of *invagination* then follows, one side of the blastula being pushed inwards to form a double-walled cup or *gastrula* (*C*) opening on the exterior by an opening, the *blastopore,* which, at first very wide, gradually becomes narrowed. At the same time the shape of the larva alters, so as to be somewhat elongated, the

blastopore, lying at first midway between the two poles, afterwards gradually drawing nearer to what becomes the posterior end.

Of the two layers of the gastrula (*D* and *E*), the outer is the *ectoderm*, the inner the *endoderm ;* between them is a space, at first filled with gelatinous matter, in which cells soon appear, giving rise subsequently to an intermediate mass of tissue, the *mesenchyme.*

The cavity in the gastrula is early distinguishable into two parts (Fig. 702, *B*)—that part into which the blastopore leads (*arch.*), and a wider terminal part (*ent.*); the former becomes the stomach and intestine of the larva, the blastopore giving rise to the larval anus; the latter is termed the *enterocœle* (*cœlome*). The wall of the enterocœle becomes thinner, and it gives off two lateral swellings,

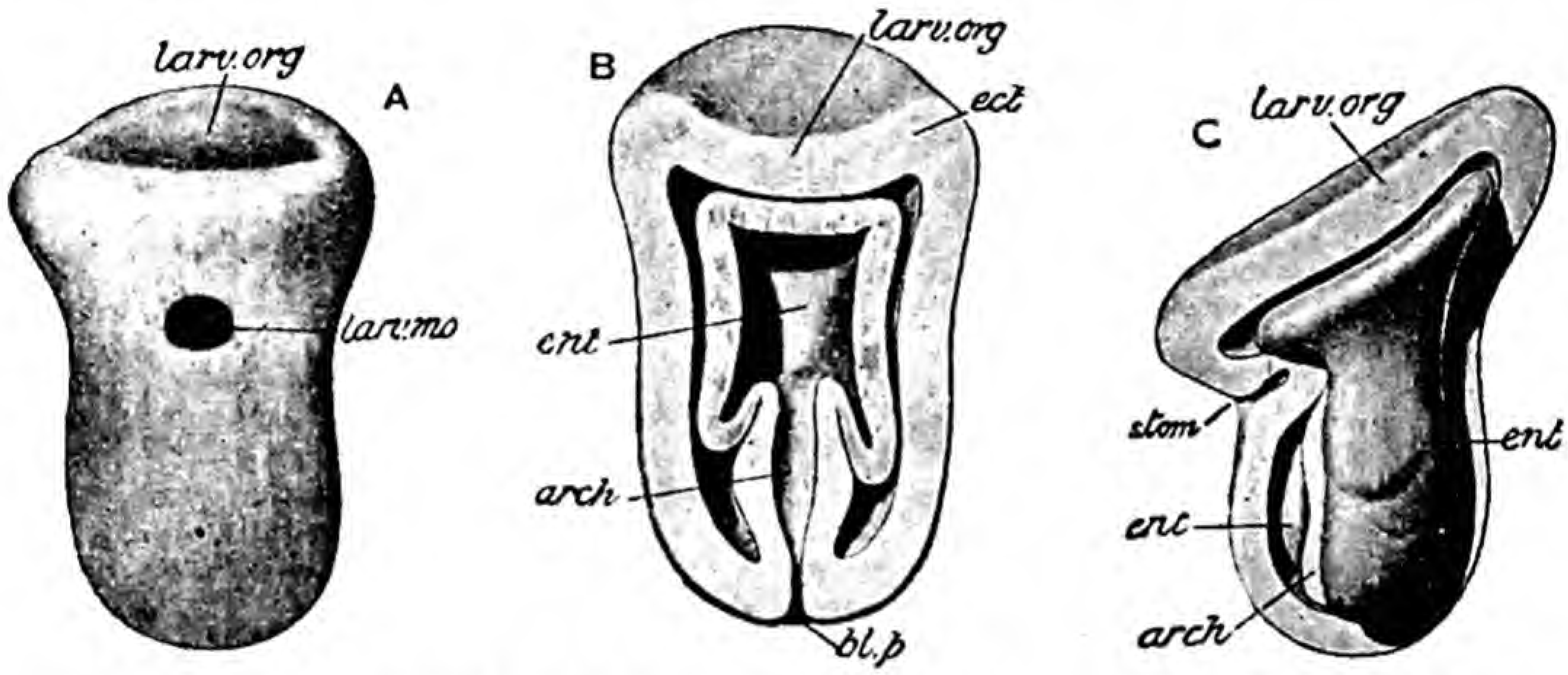


FIG. 702.—Later stages in the development of the larva of **Asterina gibbosa.** *A*, newly hatched larva, ventral surface, with the beginning of the larval organ at the anterior end and with the larval mouth. *B*, dorsal half of an embryo of the same age as *A*. *C*, somewhat older larva with larger larval organ, the ectoderm of the left side removed to expose the alimentary canal and the walls of the body-cavity. *arch.* archenteron; *bl. p.* blastopore; *ect.* ectoderm; *ent.* enterocœle; *larv. mo.* larval mouth; *larv. org.* pre-oral lobe; *stom.* stomodæum. (From Ziegler's models.)

the right and left *enterocœlic pouches* (*C*, *ent.*), which are closely applied to the sides of the larval alimentary canal: the left pouch is soon seen to be larger than the right. The enterocœle is subsequently completely closed off from the enteric canal. It now consists of three parts, an anterior undivided part, and the two pouches, right and left. Of the latter the left grows more rapidly than the right: both extend posteriorly in the space between the enteric canal and the body-wall to coalesce posteriorly in such a way as to give rise to the cœlome of the adult. The anterior undivided part (*anterior cœlome*) forms the cœlome of a conspicuous larval structure, the pre-oral lobe, and it eventually becomes cut off from the right and left pouches, giving off on the left a five-lobed outgrowth, the *hydrocœle,* which forms the foundation of the entire ambulacral system of the adult: a right hydrocœle is only represented by a small vesicle which in normal embryos undergoes no further development.

Before the hydrocœle is developed and before the right and left cœlomic pouches have become cut off, two apertures make their appearance on the surface of the larva: one, on the ventral side, is the opening of the *stomodæum* or *larval mouth;* the other, on the dorsal side, is the *dorsal pore.* The mouth subsequently opens into the larval stomach, and for a time the enteric canal of the larva opens on the exterior both by mouth and anus: soon, however, the larval anus becomes closed up. The dorsal pore is developed as an outgrowth of the anterior part of the enterocœle, a little to the left of the middle line, meeting a thickening of the ectoderm about the middle of the dorsal surface, where an aperture is formed.

The *pre-oral lobe* appears at an early stage as a dilatation at the anterior end of the larva. This takes a dorso-ventral direction, and assumes the

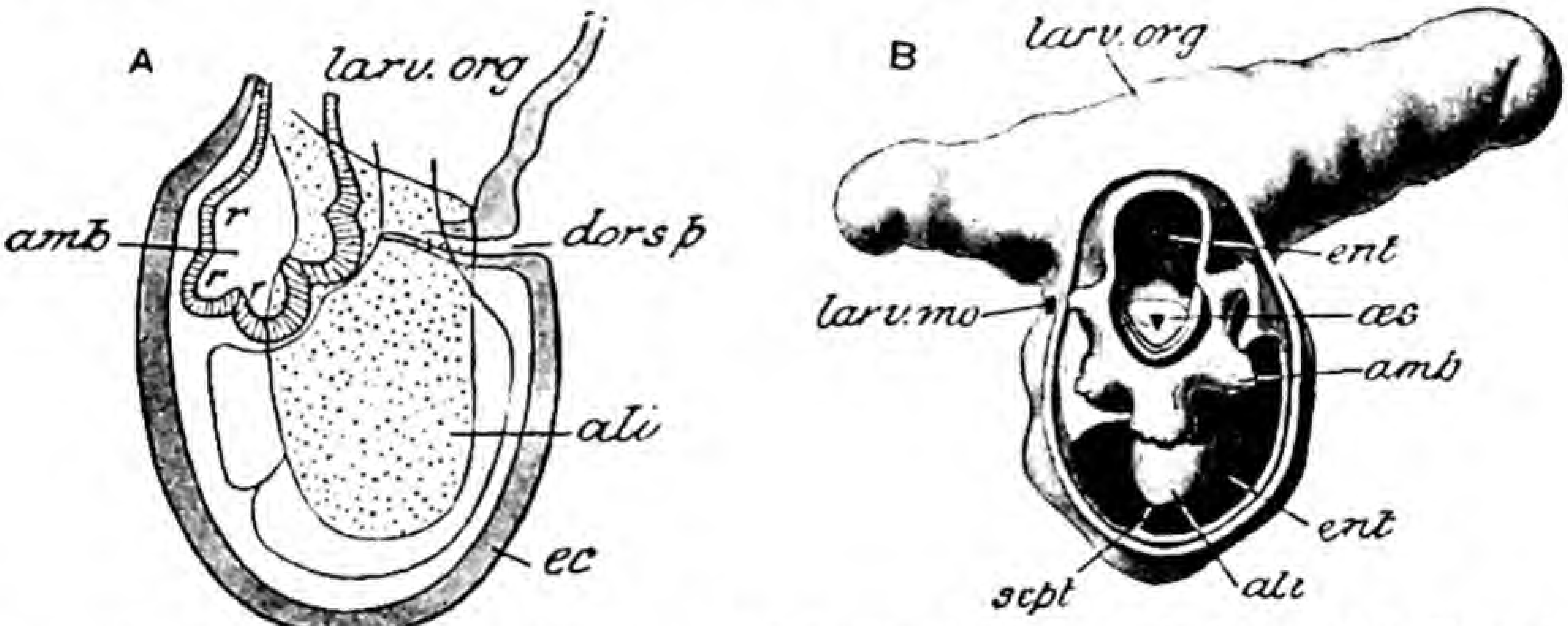


FIG. 703.—Larva of **Asterina gibbosa.** *A*, diagrammatic lateral view; the alimentary canal dotted, the ambulacral system striated, the ectoderm shaded. *B*, Larva seen from the left as an opaque object, the body-wall of the left side removed; hydrocœle separated off from left enteric sac and partly surrounding œsophagus. *ali.* alimentary canal; *amb.* ambulacral system or hydrocœle; *dors. p.* dorsal pore; *ent.* enteric sacs and cœlome; *larv. mo.* larval mouth; *larv. org.* pre-oral lobe; *œs.* œsophagus of adult; *r, r.* lobes of hydrocœle; *sept.* septum between the enterocœlic sacs. (*A*, after Ludwig; *B*, from Ziegler's models.)

character of an elongated, almost cylindrical, hollow appendage at the anterior end of the larva, consisting of a shorter ventral, and a longer dorsal, part. On the anterior surface of the pre-oral lobe a flattened area appears surrounded by a raised rim, which is beset with specially large cilia: this is the *larval organ.* In the middle of the larval organ appears an elevation, the rudiment of a sucker by means of which the larva becomes attached when the metamorphosis is about to begin. At this stage the larva (Fig. 704) is able to creep by contractions of the pre-oral lobe, and also by the action of the cilia, more especially the cilia of the larval organ.

The hydrocœle, at first a five-lobed outgrowth of the enterocœle, grows into the form of a horse-shoe with five lobes, each of which represents one of the radial parts of the ambulacral system, the horse-shoe itself representing the ring-vessel. The rudiment of the madreporic canal arises as a groove on the posterior wall of the anterior cœlome. This develops into a canal leading from

the hydrocœle to the anterior cœlome, and eventually entering into connection with the dorsal pore, forms a tube, the madreporic canal, leading from the ring canal to the madreporite, of which the dorsal pore represents the first-formed aperture.

As the hydrocœle develops, its form influences the external shape of the larva; on the left-hand side there grows out a five-lobed elevation (Fig. 704, *amb.*), each of the lobes corresponding to one of the five lobes of the hydrocœle. Each lobe of the hydrocœle then becomes divided, first into three rounded processes, and then into five, and these project freely on the surface; the middle one is the rudiment of the tentacle, the lateral processes are the first two pairs of tube-feet. At the same time five elevations of the opposite body-wall of the larva become evident, and give rise to the beginnings of the dorsal regions of the arms (Fig. 706).

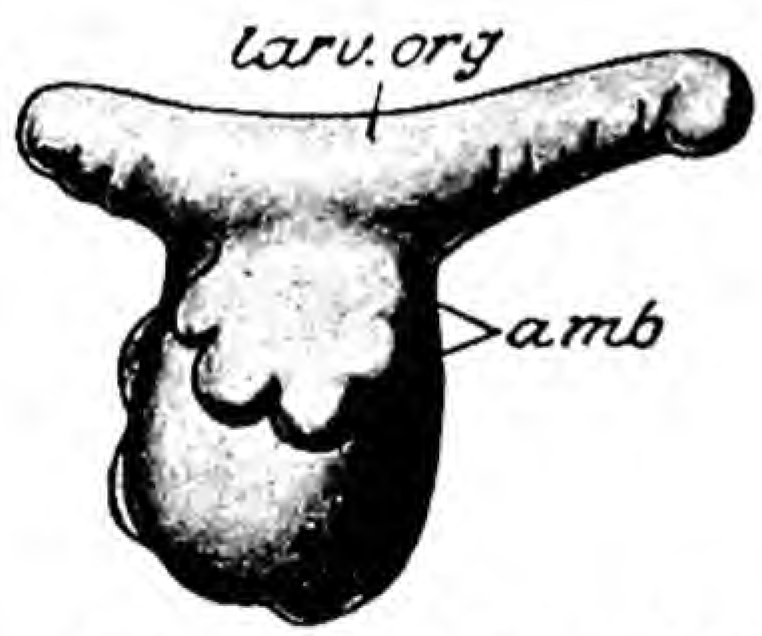


FIG. 704.—Larva of **Asterina**, view of the left side, showing the five-lobed prominence (*amb.*) formed by the developing ambulacral system on what is destined to become the ventral surface of the body of the Starfish; *larv. org.*, pre-oral lobe with larval organ.

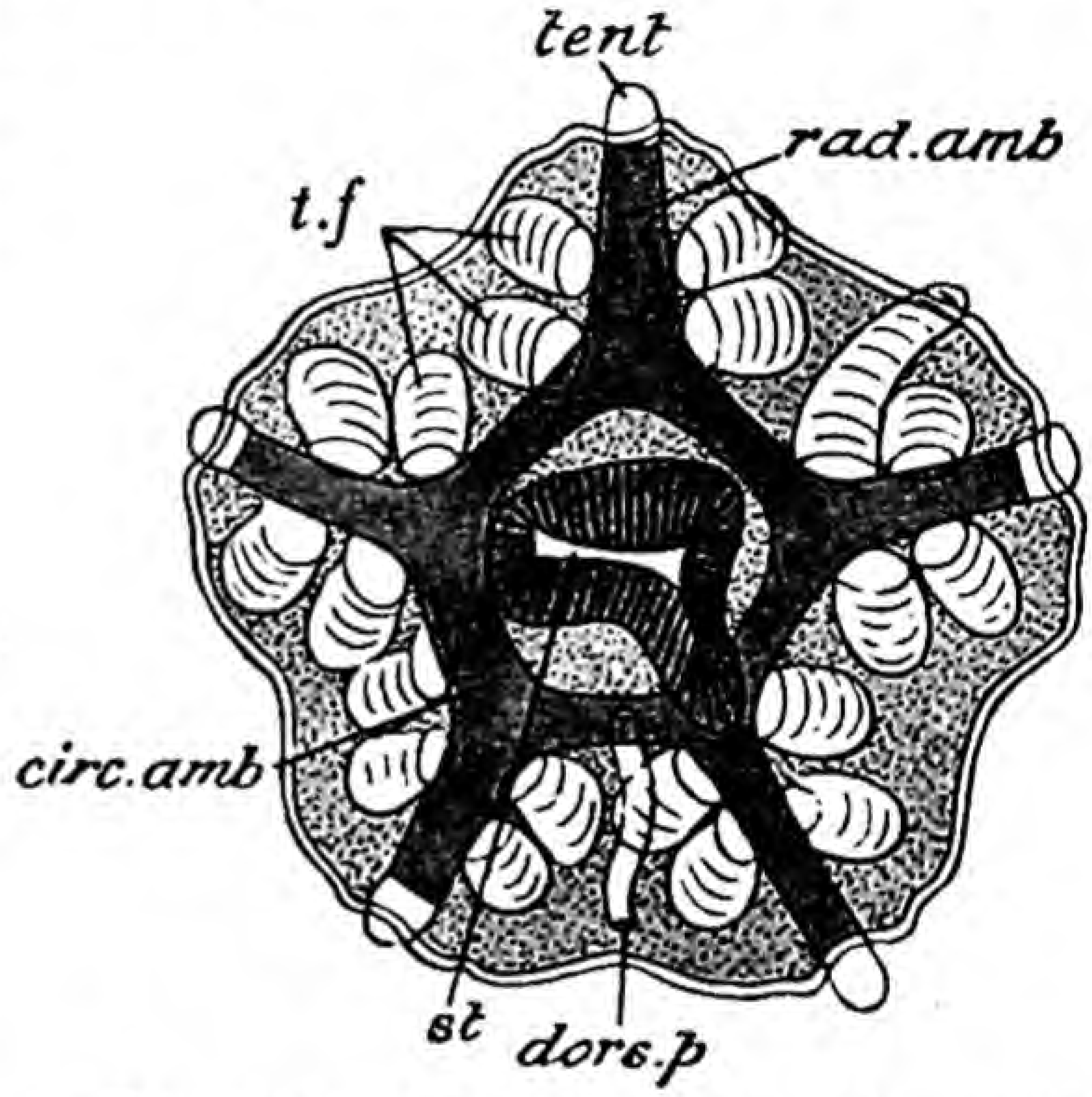


FIG. 705.—**Asterina exigua.** Young Starfish shortly after the metamorphosis has been completed, viewed from the oral side. *circ. amb.* circular ambulacral vessel; *dors. p.* dorsal pore and madreporic canal; *rad. amb.* radial ambulacral vessel; *st.* stomach; *tent.* tentacle; *t. f.* tube-feet.

The transition from the larval stage to the condition of the five-rayed Starfish (Fig. 705) is effected by the abortion of the pre-oral lobe—(which, on the larva becoming fixed by means of the sucker, degenerates into a temporary stalk and eventually becomes completely absorbed)—by the further development of the arms and tube-feet, and by certain changes which take place in the internal organs. Of these, one of the most important is the formation of a new mouth and œsophagus (Fig. 703, *B*, *œs.*), the larval mouth and œsophagus becoming abolished during the metamorphosis. The new mouth is formed in the centre of the hydrocœle (ring-vessel). From the stomach, diverticula grow out radially into the developing arms to give rise to the cæca; and later the permanent anal opening is formed on the dorsal surface.

The perihæmal system takes its origin from five cœlomic outgrowths giving

rise to the radial perihæmal vessels and the external part of the oral ring-vessel. The inner division of the ring-vessel and the axial sinus connected

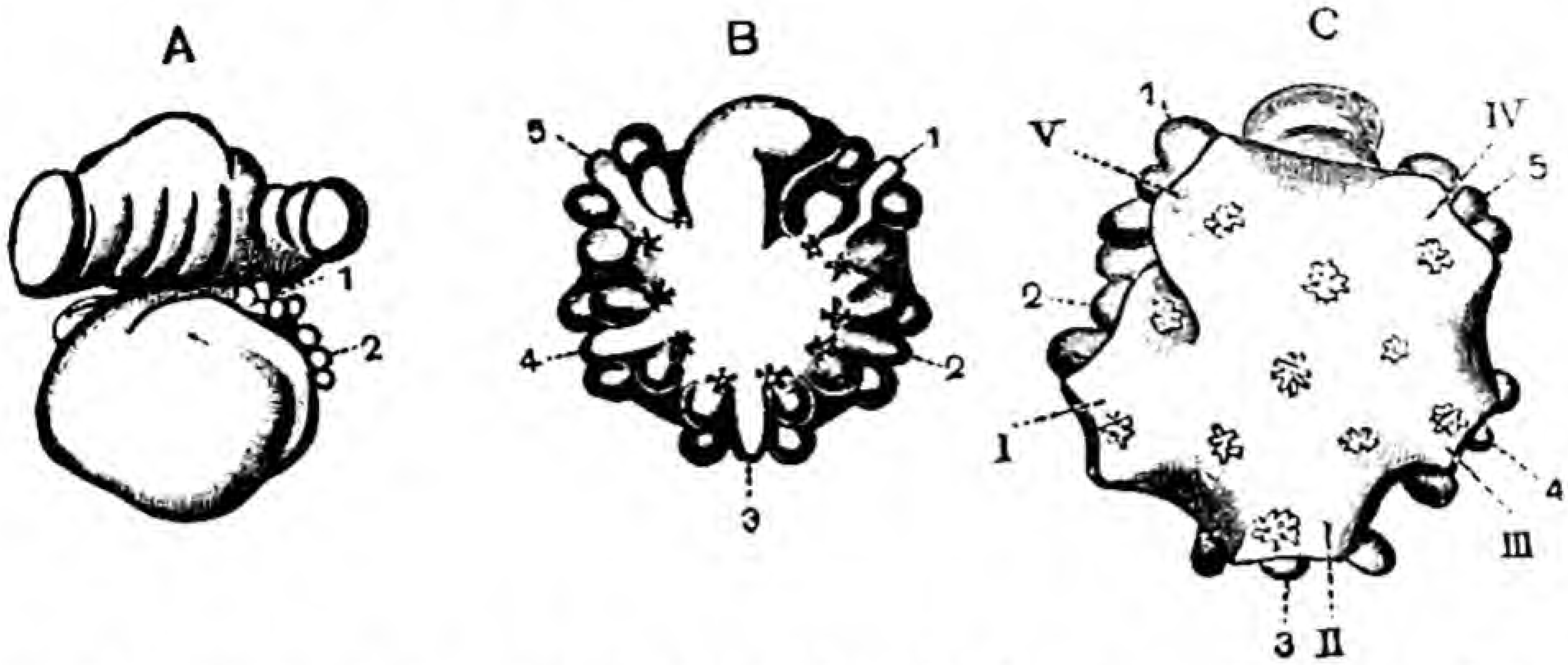


FIG. 706.—Views of the larva of **Asterina gibbosa** in the course of metamorphosis. *A*, larva of eight days, from the right; *B*, left, and *C*, right view of the larva of nine days; 1—5, lobes of hydrocœle; I—V, rudiments of arms. (From MacBride, after Ludwig.)

with it are formed by the posterior part of the anterior cœlom, which becomes incorporated in the body of the Starfish during metamorphosis.

When the first ossicles are definitely formed they present the following arrangement (Fig. 707). In the middle of the abactinal surface is a single

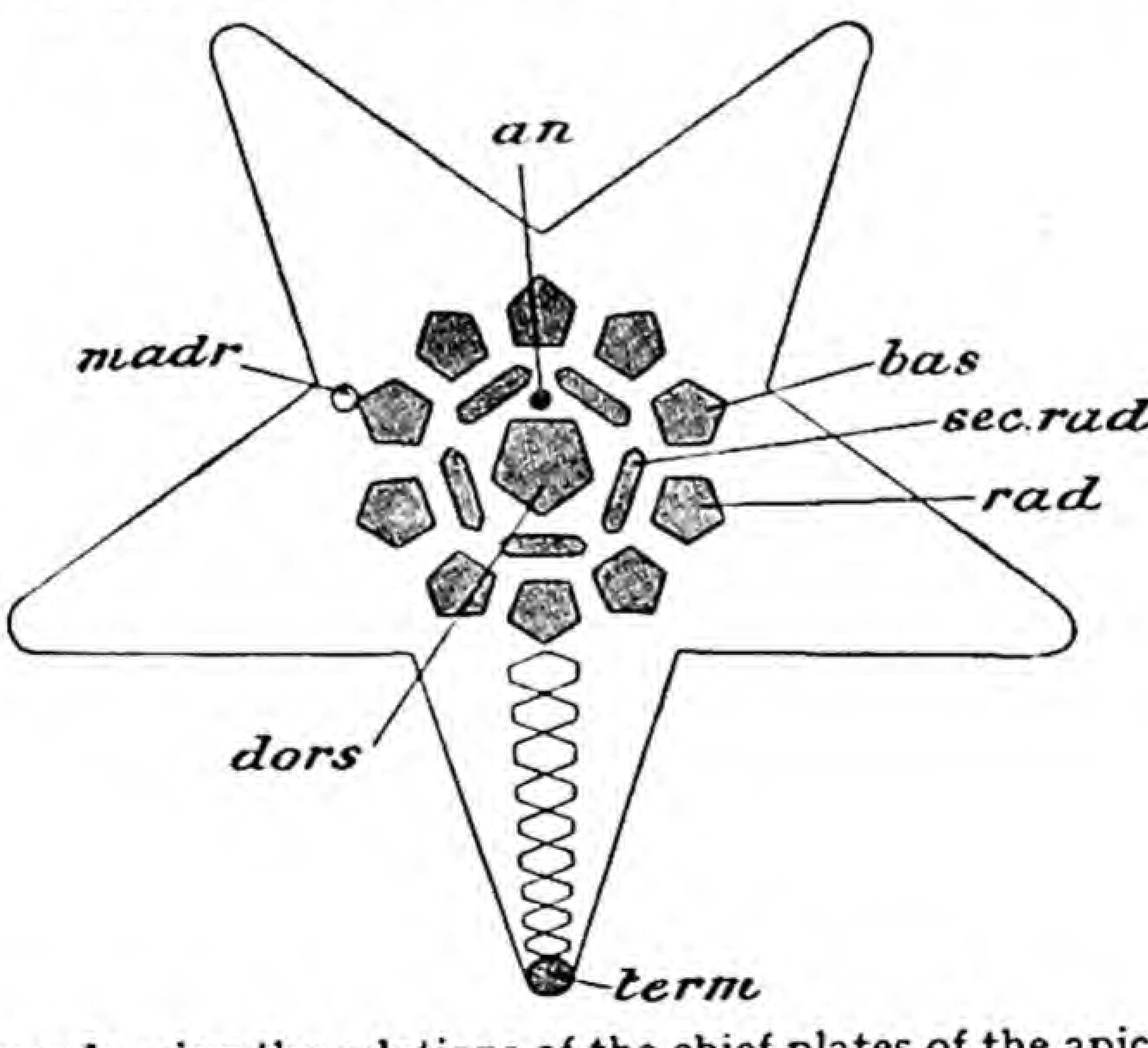


FIG. 707.—Diagram showing the relations of the chief plates of the apical system in the young **Starfish.** *an.* anus; *bas.* basals; *dors.* central; *madr.* madreporite; *rad.* radials; *sec. rad.* secondary radials (infra-basals); *term.* terminal.

central plate (*dors.*). Around this are five *basals* (*bas.*) one of which becomes merged into the madreporite. External to these, five *radials* (*rad.*) appear somewhat later. At the end of each developing arm is a single *terminal* or ocular plate (*term.*), which is carried outwards as the ambulacral and adambul-

acral ossicles of the arm are developed, supporting the corresponding eye and tentacle. A ring of *secondary radials* or *infra-basals* (*sec. rad.*) is developed between the radials and the central. In the adult, by the intercalary development of numerous additional ossicles, these primary plates of the *apical system*, as it is termed, lose their original arrangement, and become no longer recognizable.

2. Example of the Echinoidea.

A Sea-urchin.—(*Strongylocentrotus* or *Echinus*.)

General External Features.—The Sea-urchin (Figs. 709 and 710) is globular in shape, but somewhat compressed in one direction, so that two *poles* are distinctly recognizable. At one of these the degree of flattening is greater than

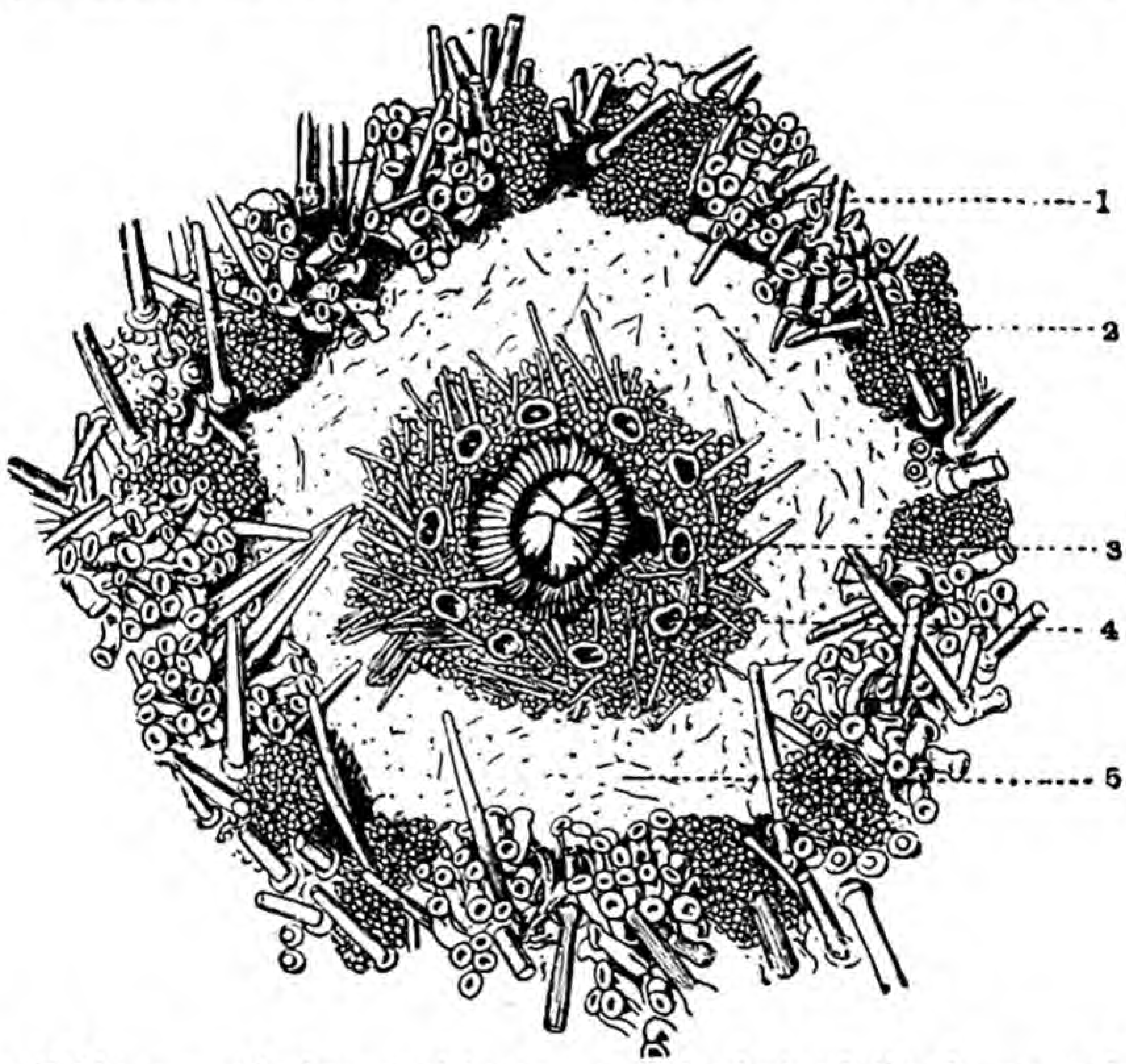


FIG. 708.—**Echinus esculentus,** peristome. 1, tube-feet of the lower ends of the radii; 2, branchia; 3, teeth; 4, oral tube-foot (tentacle); 5, peristomial membrane. (From MacBride after Kükenthal.)

at the other; this is the *oral pole*, the opposite pole being termed the *anal* or *aboral*. At the oral pole is a rounded aperture, the *mouth*, through which may be seen projecting five hard white points, the extremities of the *teeth*; surrounding the mouth is a thin, soft membrane known as the *peristome* or *peristomial membrane* (Fig. 708). At the anal pole is a much smaller aperture, the *anus*, the space immediately surrounding which is termed the *periproct* (Fig. 710).

The entire surface, with the exception of the peristome and periproct, is bristling with spines—cylindrical, pointed, solid appendages, the surface of which is longitudinally fluted. These are movably articulated with the body so that they may be turned about in all directions. When one of them is removed (see Fig. 725, p. 730), it is found that the joint is of the character of a ball and socket, a concavity on the base of the spine fitting over a hemispherical elevation on the surface of the Sea-urchin, and the spine being retained in place and caused to move by means of a capsule of muscular fibres enclosing

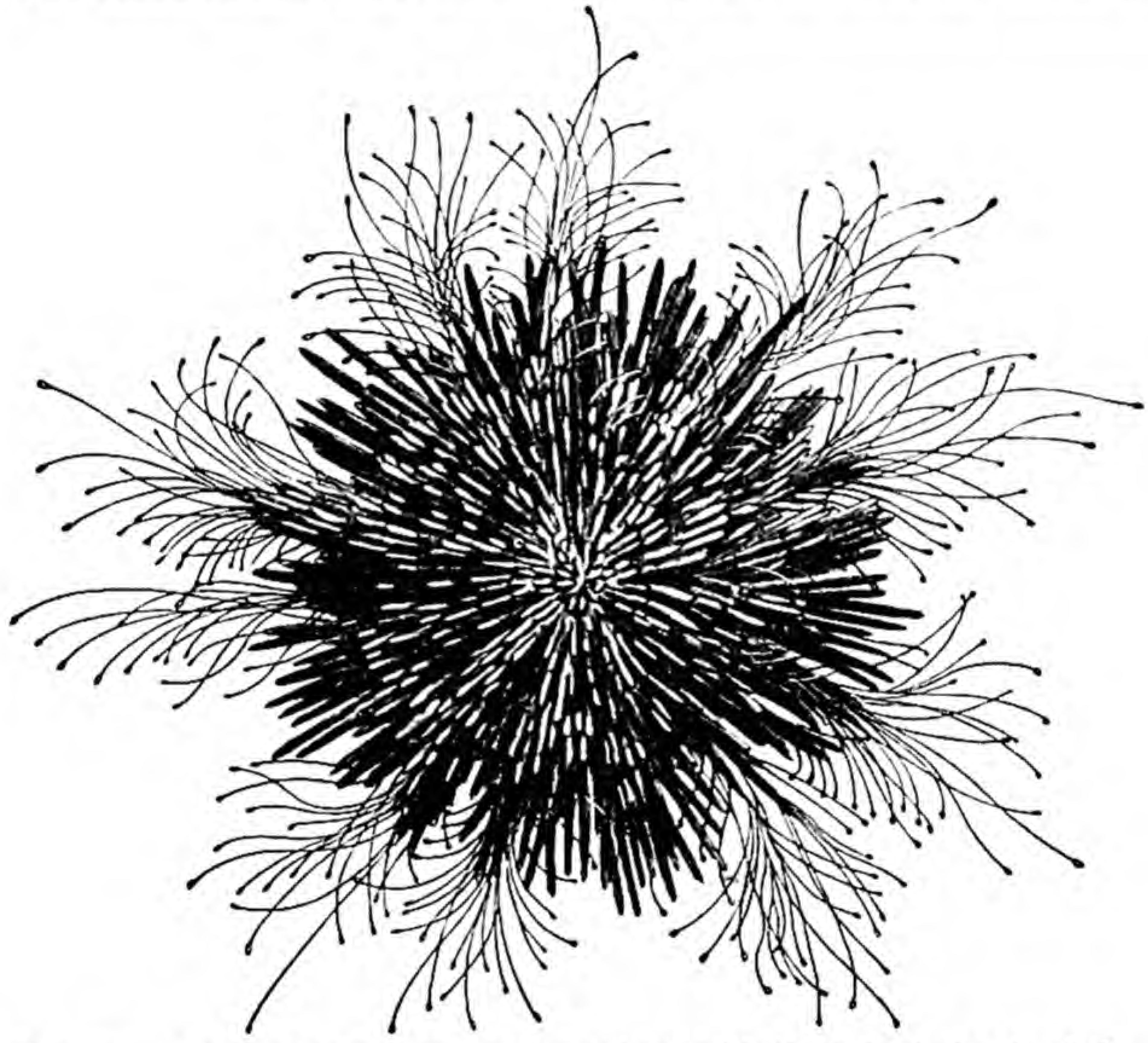


FIG. 709.—**Strongylocentrotus**, entire animal with the tube-feet extended. (From Brehm's *Tierleben*.)

the joint. Around the bases of the large spines are a number of very small spinules. Here and there among the spines are to be observed minute *pedicellariæ* (see Fig. 726, p. 730), which are comparable to the stalked pedicellariæ of Asterias; but each has three jaws instead of two, and a relatively long stalk, which is supported by a slender calcareous rod. Here and there are to be found also small rounded bodies termed the *sphæridia*, which are perhaps, like the pedicellariæ, to be looked upon as modified spines: they contain ganglion-cells and are apparently sense-organs.

Projecting from the surface among the spines all the way from the peristome to the periproct will be observed five double rows of *tube-feet* or *podia* (Fig. 709),

which in a living specimen will be found to be capable of great extension. These are similar to the tube-feet of the Starfish, and have similar functions: the sucker-like extremity of each is supported by a plate of calcareous matter. Each double row of tube-feet occupies a meridional zone of the surface, termed the *ambulacral area*, corresponding to the ambulacral groove of the Starfish: the intermediate zones are termed the *inter-ambulacral areas*. At the oral end of each ambulacral area on the peristome (Fig. 708, 4) is a pair of appendages similar to tube-feet, but shorter, and termed *oral tentacles*. Ten shrub-like

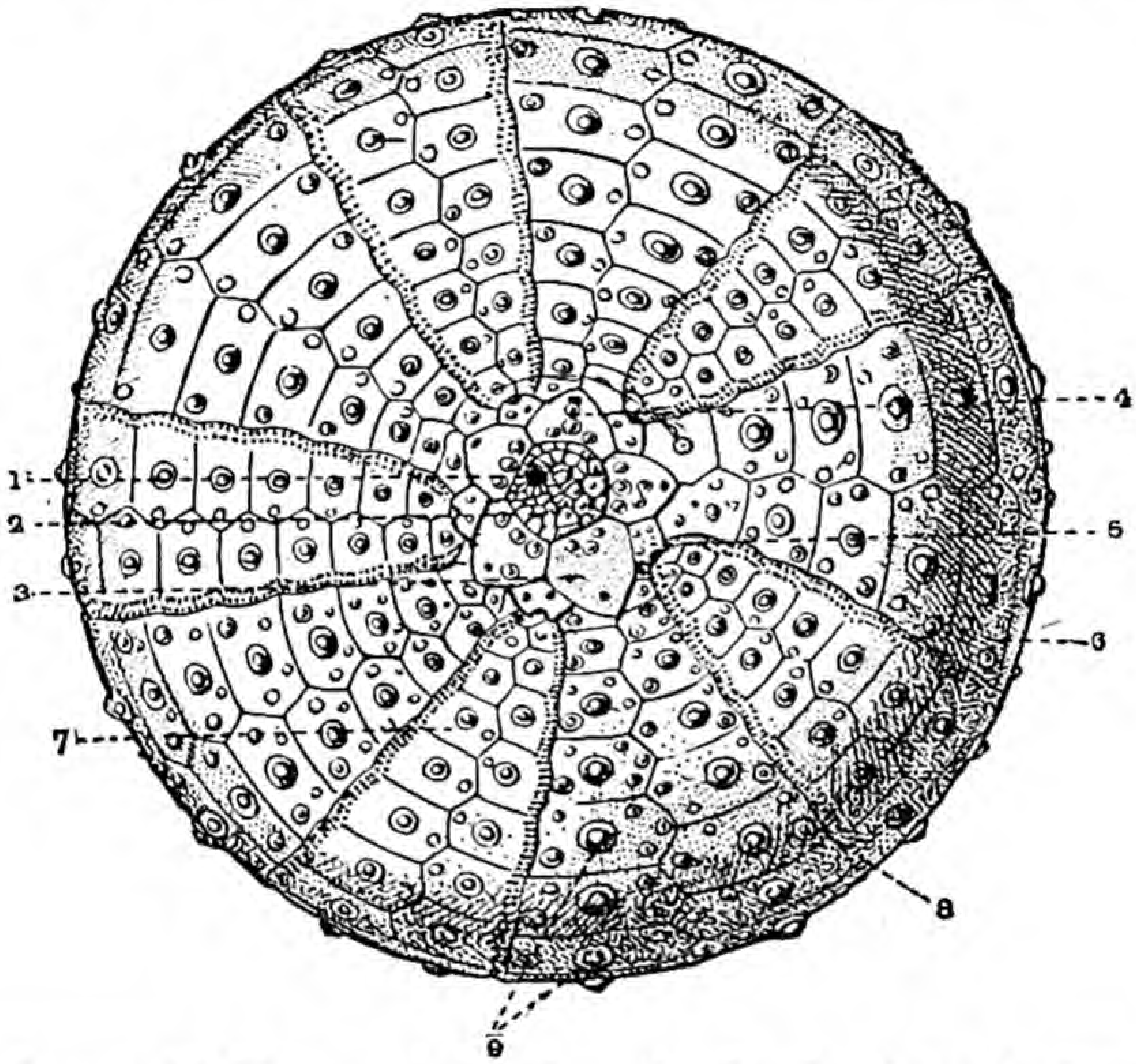


FIG. 710.—Corona of **Echinus esculentus**, from the aboral surface, showing the arrangement of the plates of the corona. 1, the anus; 2, periproct, with irregular plates; 3, the madreporite; 4, one of the other genital plates; 5, an ocular plate; 6, an inter-ambulacral plate; 7, an ambulacral plate; 8, pores for the protrusion of the tube-feet; 9, tubercles. (After MacBride.)

appendages, the *dermal branchiæ* (2), are situated in the peripheral part of the peristome, a pair opposite each inter-ambulacral area.

When the spines are removed, the body is found to be enclosed in a rigid globular shell, or **corona** (Fig. 710) as it is termed, formed of a system of plate-like ossicles, the edges of which fit accurately and firmly together, and the surfaces of which are ornamented with the rounded elevations or tubercles for the articulation of the spines. These plates are arranged in ten zones, each consisting of two rows, running in a meridional direction from the edge of the peristome to the neighbourhood of the periproct. Of the zones of plates there are two sets, each consisting of five, the members of which alternate with one another. In the case of one of these sets of zones—the *ambulacral zones* or

ambulacral areas already referred to—each of the plates is perforated towards its outer end by two minute pores, the *ambulacral pores*, for the protrusion of the tube-feet. In the other five zones, the *inter-ambulacral zones* or *areas*, the plates are not perforated. At its anal end each area, ambulacral or inter-ambulacral, ends in a single *apical* plate, so that the periproct is surrounded by a ring of ten plates, the *apical system* of plates. Of these, the five that are situated at the ends of the ambulacral areas are termed the *ocular plates* (5), owing to the fact that each of them bears a structure once supposed to be a rudimentary eye, but now known to be a tentacle; while the five opposite the inter-ambulacral areas are termed the *genital plates* (4), each of them being perforated by an opening which is the aperture of one of the five *genital ducts* —the ducts of the ovaries or testes as the case may be. One of these genital plates (3) has a swollen and spongy appearance, which distinguishes it from the

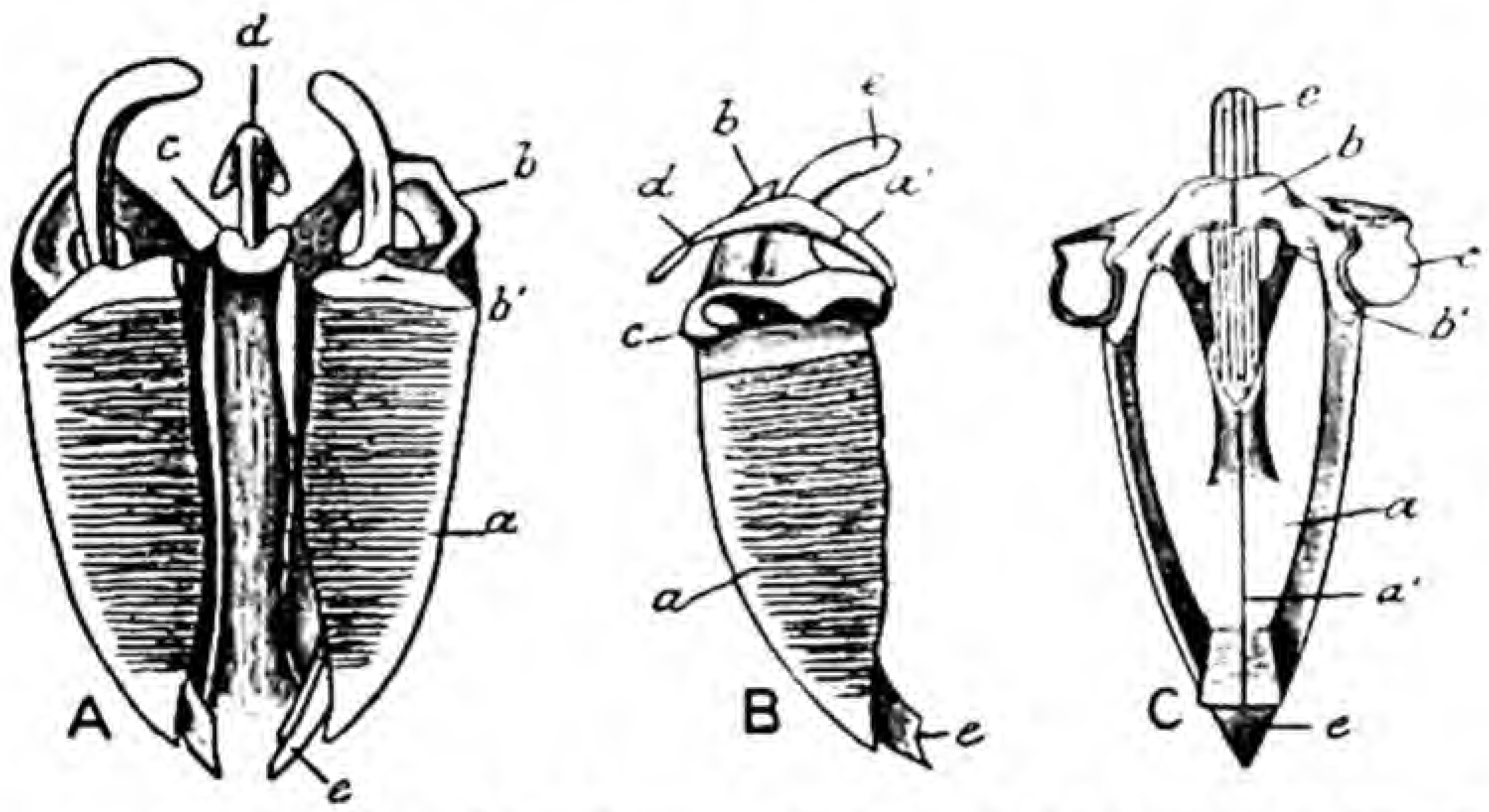


FIG. 711.—Lantern of Aristotle of **Echinus.** *A*, two of the five chief component parts apposed and viewed laterally. *B*, lateral, and *C* internal view of a single part. *a*. alveolus, and *a'*. suture with its fellow; *b*. epiphysis; *b'*. suture with alveolus; *c*. rotula; *d*. radius; *e*. tooth. (From Huxley's *Invertebrates*, after Müller.)

others: this is the *madreporite*, through which, as in the case of the structure of the same name in the Starfishes, the madreporic canal communicates with the exterior. The two ambulacral areas between which the madreporite lies constitute the *bivium*, the remaining three the *trivium*.

On the inner surface of the shell, close to the edge of the peristome, there project inwards five processes, the *auricles* (Fig. 712, *aur.*), one opposite each ambulacral area. Within the ring of auricles lies a complex structure termed **Aristotle's lantern** (Fig. 711). This consists of the five teeth (*e.*), the apices of which are to be seen projecting through the mouth, together with a system of ossicles. The teeth are long, curved, and pointed: proximally each is supported by and partly embedded in a pyramidal ossicle, the *alveolus* (*a.*), consisting of two halves united by a longitudinal suture. Firmly united to the base of the alveolus is a stout bar, the *epiphysis* (*b.*). Adjacent epiphyses are in close contact with one another, and running inwards from their points of

union are five radially-directed, stout bars, the *rotulæ* (*c.*), the inner ends of which unite to bound a circular aperture through which the œsophagus passes. With the inner end of each rotula is movably articulated a more slender bar, the *radius* (*d*), which runs outwards, parallel with, and closely applied to, the rotula, to end in a free, bifurcated extremity. Aristotle's lantern as a whole is in the shape of a five-sided pyramid, at the apex of which project the five teeth; the pyramid is hollow, containing a passage which is the beginning of the œsophagus. The base has the appearance of a wheel, the tyre of which is represented by the five epiphyses, the spokes by the five rotulæ with the five

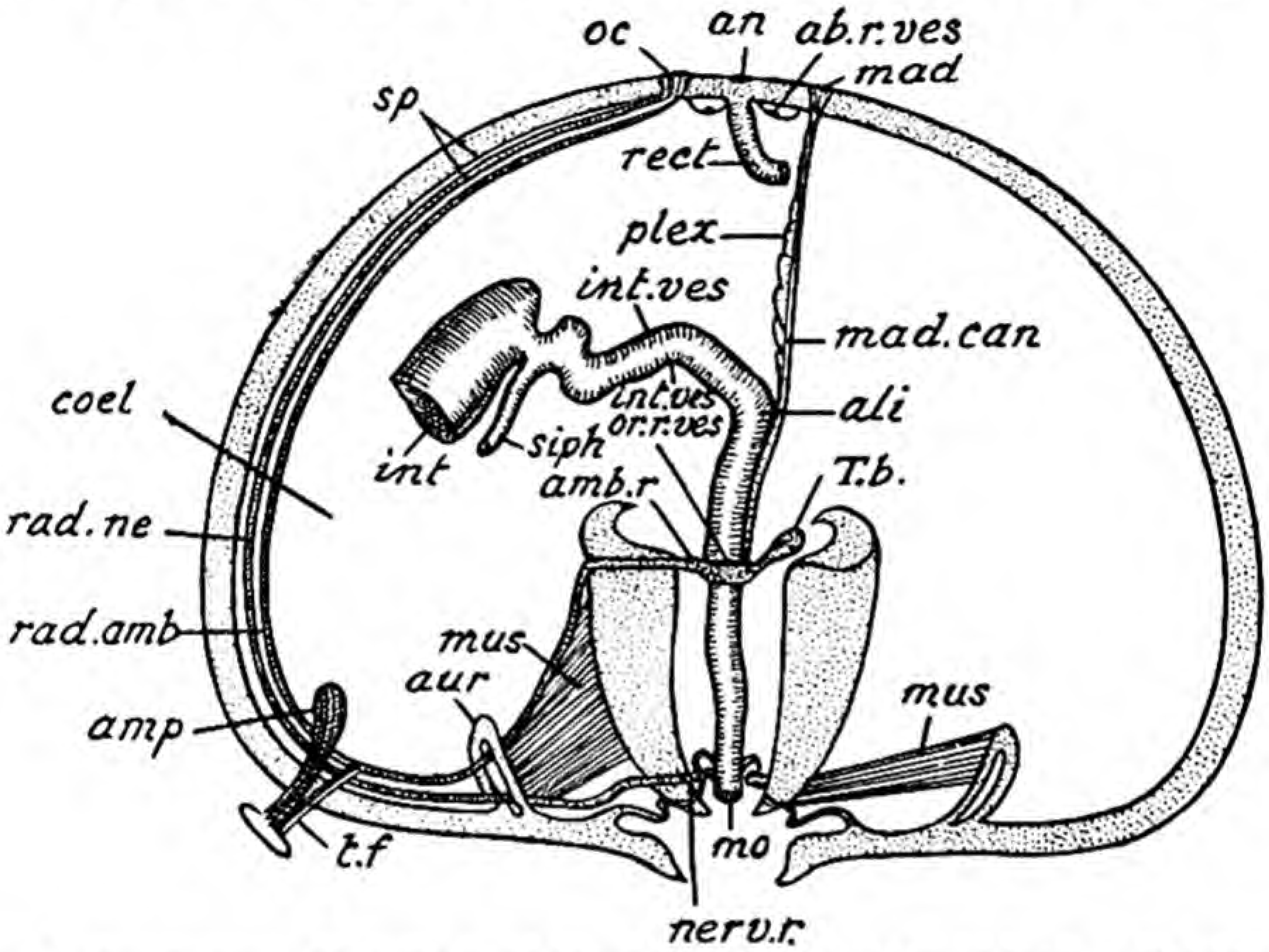


FIG. 712.—Lateral view of the internal organs of a **Sea-urchin** as seen on the removal of a half of the shell. *ab. r. ves.* hæmal strand, aboral ring; *amb. r.* ambulacral ring-canal; *amp.* ampullæ; *an.* anus; *aur.* auricle; *cœl.* cœlome; *int.* intestine; *int. ves.* intestinal hæmal strands; *mad.* madreporite; *mad. can.* madreporic canal; *mo.* mouth; *mus.* muscles passing from the auricles to Aristotle's lantern; *nerv. r.* nerve-ring; *oc.* ocular plate; *or. r. ves.* hæmal strand, oral ring; *plex.* axial organ; *rad. amb.* radial ambulacral vessel; *rad. ne.* radial nerve; *siph.* siphon; *sp.* radial extension of the cœlome surrounding the nerve; *T. b.* Tiedemann's bodies; *t. f.* tube-feet. (After Hamann.)

radii in close contact with them, and the hub by the rounded central aperture. Passing between the various ossicles of the lantern, and from them to the auricles, are systems of muscles by means of the contractions of some of which the lantern as a whole can be protruded or retracted, while the action of others is to cause the movements of the alveoli by which the teeth are brought to bear on the food.

Nervous System.—Passing outwards through each auricle, and running along the inner surface of the corona opposite the middle of each ambulacral area, is a *radial nerve* (Fig. 712, *rad. ne.*). Within the ring of auricles the five radial nerves are connected with a *nerve-ring* (*nerv. r.*) surrounding the mouth.

At its distal end each radial nerve is connected with the so-called *eye* (*oc.*), borne by the corresponding ocular plate. These parts correspond to the *epidermal* nervous system of the Starfish, which, owing to the ambulacral grooves having become closed in to form narrow canals—the *epineural canals* (Fig. 713, *ep.*), covered over by the plates of the corona—is here more deeply situated; the deep and cœlomic systems are only feebly developed.

Ambulacral System.—Internal to each radial nerve, and pursuing a corresponding course, runs a *radial ambulacral vessel* (Figs. 712 and 713). From this are given off on each side a series of short branches to the tube-feet, with each of which is connected one of a series of compressed sacs, the *ampullæ*

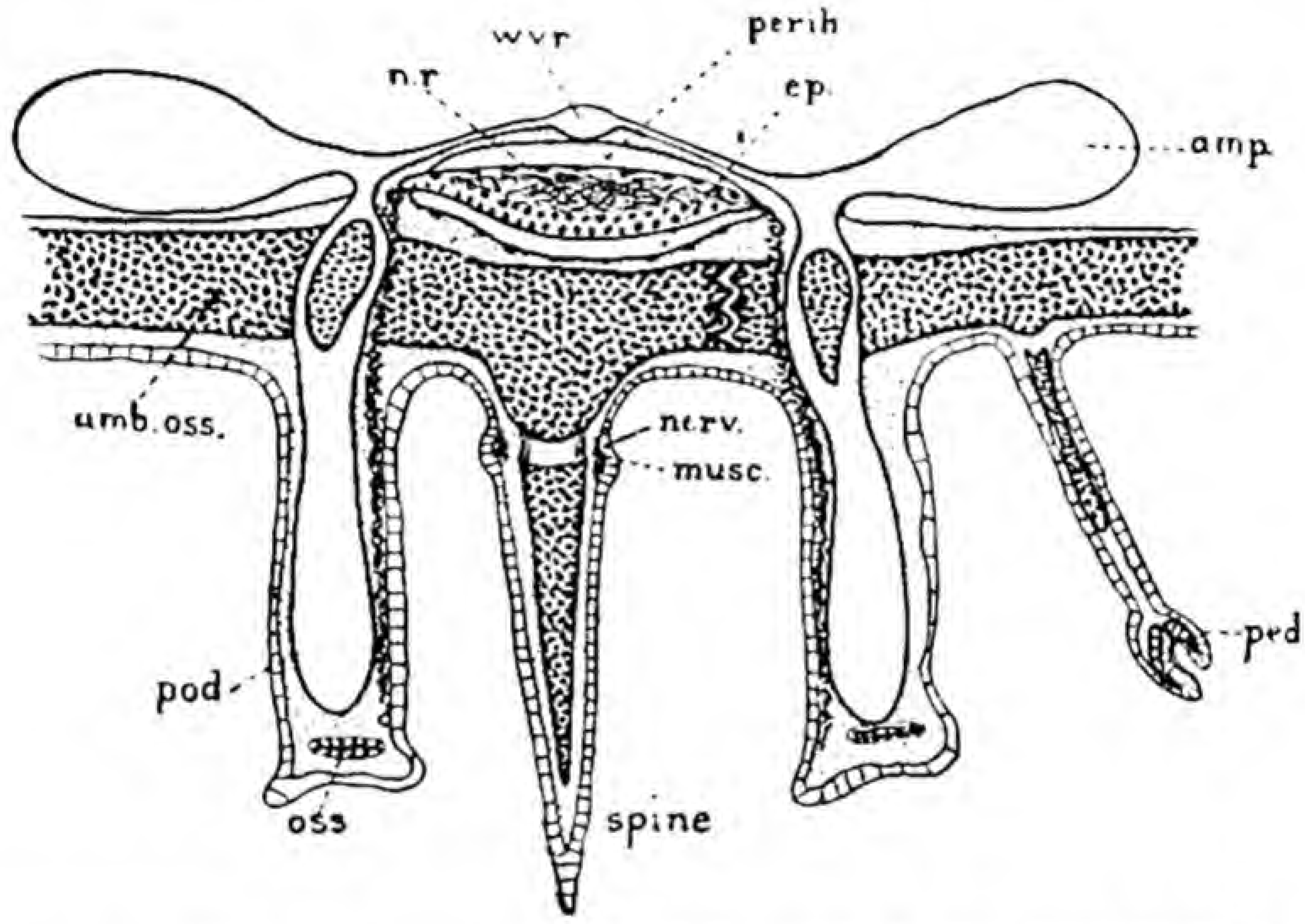


FIG. 713.—Diagrammatic transverse section of the ambulacral zone of an **Echinoid.** *amb. oss.* ambulacral ossicle; *amp.* ampulla of a tube-foot; *ep.* epineural canal; *musc.* muscles attaching spine to its tubercle; *nerv.* nervous ring in base of spine; *n. r.* radial nerve-cord; *oss.* ossicle in the sucker of the tube-foot; *ped.* pedicellaria; *perih.* radial perihæmal canal; *pod.* tube-foot; *wv. r.* radial ambulacral vessel. (After MacBride.)

(*amp.*), by two canals, one passing through each of the two pores. At their oral extremities the five radial ambulacral vessels unite with a *ring-vessel* surrounding the œsophagus. Appended to the ring-vessel are five small mammillated bodies, the so-called Tiedemann's bodies (Fig. 712, *T. b.*). A *madreporic canal* (*mad. can.*), corresponding to that of the Starfish, but with soft membranous walls devoid of ossicles, runs from the madreporite at the side of the periproct to the ring-canal.

The **enteric canal** (Fig. 714, *ali.*) is devoid of the radial cæca which it presents in the Starfish: it is a wide, soft-walled tube, which winds round the interior of the corona in its passage from the mouth to the anus, held in place by a band of threads, the *mesentery*, passing out from it to the inner surface of the shell. It gives off a short diverticulum, the *siphon* (*siph.*), which opens into it

at both ends; this, together with the intestine itself, probably acts as an organ for the respiration of the cœlomic fluid.

The **cœlome** contains a fluid in which, as in the Starfish, there are numerous corpuscles. Of these there are two kinds—*amœboid corpuscles* (*amœbocytes*) with long pseudopodia, and *vibratile corpuscles*, which closely resemble sperms, having a rounded head and a slender vibratile tail: the latter aid in bringing about a constant circulation of the cœlomic fluid.

The part of the cœlome containing Aristotle's lantern is completely cut off from the rest by the arrangement of the membrane enclosing the lantern, and

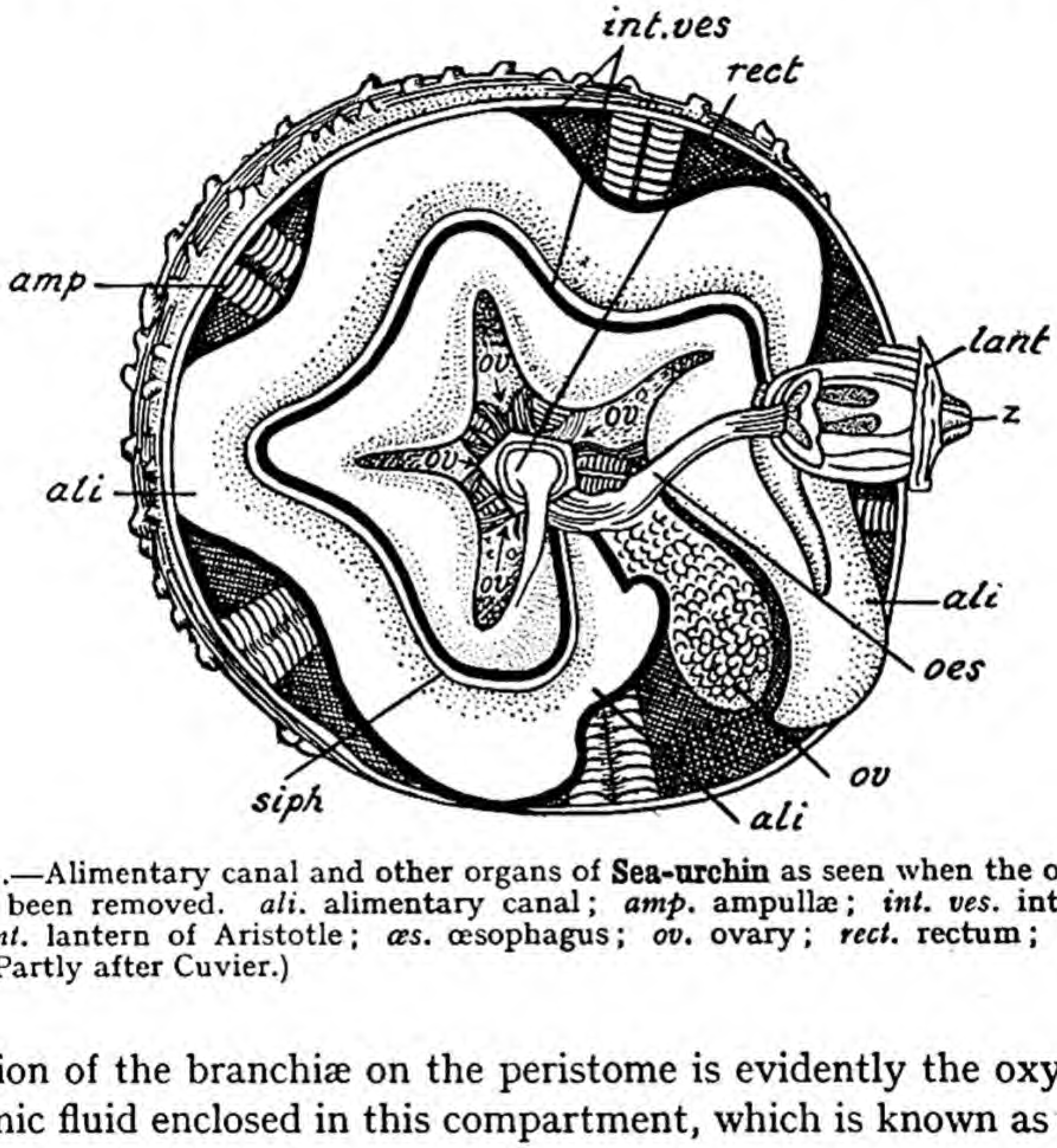


FIG. 714.—Alimentary canal and other organs of **Sea-urchin** as seen when the oral half of the corona has been removed. *ali.* alimentary canal; *amp.* ampullæ; *int. ves.* intestinal blood-vessels; *lant.* lantern of Aristotle; *œs.* œsophagus; *ov.* ovary; *rect.* rectum; *siph.* siphon; *z.* teeth. (Partly after Cuvier.)

the function of the branchiæ on the peristome is evidently the oxygenation of the cœlomic fluid enclosed in this compartment, which is known as the *lantern-cœlome.*

The **perihæmal** and **hæmal** or **lacunar** systems, as well as the *axial organ*, will be referred to in the account of the general structure of the phylum.

The **reproductive organs** consist of five masses of minute rounded follicles (Fig. 714, *ov.*) situated in the anal portion of the shell, and each communicating with the exterior by its duct, which perforates the corresponding genital plate. The sexes are distinct; as in the Starfish, there is little difference to be observed between the ovaries of the female and the testes of the male until we come to examine their microscopic structure. The genital rachides which in the

Starfish connect the gonads with the genital stolon (p. 697) are aborted in the adult Sea-urchin.

The early stages in the **development** of the Sea-urchin are very similar to the corresponding stages in the development of the Starfish described on page 698. The bilateral larva of the Sea-urchin, which is termed a *pluteus*, is provided with a number of elongated arms or processes supported by delicate calcareous rods. A metamorphosis in which the bilateral larva becomes converted into the radial adult, takes place as in the Starfish.

3. Example of the Holothuroidea.

A Sea-cucumber.—*Cucumaria* or *Colochirus*.

General External Features.—The body (Fig. 715) is elongated, in shape not unlike a miniature cucumber, somewhat irregularly five-sided, with an opening at each end. One end is somewhat thicker than the other, and the opening at this thicker (oral or anterior) end is the *mouth*, that at the opposite (aboral or posterior) end is the *anus*. The body is five-sided, and along each side there extends a double row of *podia* or *tube-feet*. In Colochirus there is a very distinct *ventral* surface, into which three of the five sides enter, distinguished by the absence of the rows of tubercles that occur on the dorsal portion of the surface, and by the presence of three distinct bands of tube-feet. This ventral part of the body with its three ambulacral areas is the equivalent of the *trivium* of the Starfish, the rest representing the *bivium*. On the dorsal surface, instead of typical tube-feet, there are papillæ devoid of sucking extremities, and similar appendages take the place of tube-feet at the ends of the three ventral bands. In Cucumaria the ventral surface is less distinctly defined, but its position is to be determined by reference to the tentacles; there are no papillæ. The ventral surface is, it is to be noticed, *parallel* with the axis joining mouth and anus, and the body, when compared with that of the Starfish or Sea-urchin, is greatly drawn out in the direction of the line joining mouth and anus.

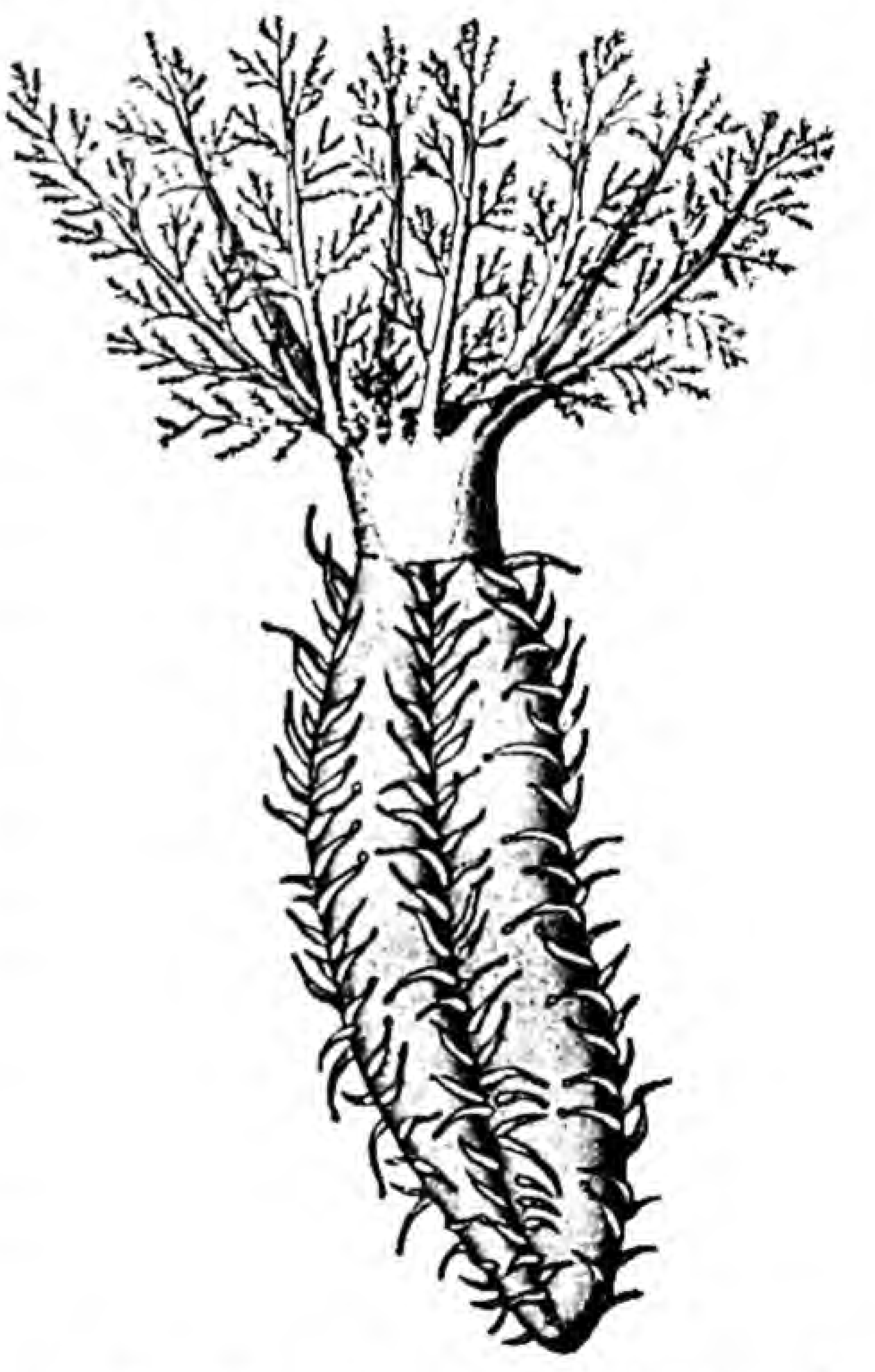


Fig. 715.—**Cucumaria planci.** Entire animal seen from the ventral surface. (From Hertwig's *Lehrbuch*, after Ludwig.)

There are no definite calcareous plates; but the integument is tolerably

hard, owing to the presence in its substance of innumerable microscopic calcareous *spicules*, very variable in shape in different species of Cucumaria, and in Colochirus having the form of sieve-like or lattice-like plates, some of which are to be found even in the walls of the tube-feet. The tube-feet are, like those of the Starfish, used in locomotion, progression being effected by creeping with the ventral surface applied to the ground. In a Sea-cucumber living undisturbed under natural conditions there will be found protruding through the mouth a circlet of ten *tentacles*, which are to be looked upon as greatly developed and specially modified podia. These are tree-like in shape —a central stem giving off a number of short branches, which may in turn be branched—and they are highly sensitive and contractile. The tentacles are withdrawn by means of retractor-muscles situated around the œsophagus. Two of these tentacles will be seen to correspond to each of the ambulacral areas. The pair situated opposite the middle ambulacral area of the ventral surface are very much smaller than the others, and will be observed to perform the special function of pushing the food-particles into the mouth. All the tentacles are drawn completely back within the mouth when the animal is disturbed.

Structure of Body-wall.—When the wall of the body is divided, it is found to consist, in addition to the hardened *integumentary* layer, of two layers of *muscle* in addition to a thin layer of cells, the *peritoneum* or *cœlomic epithelium*, lining the cœlome. The outer layer of muscle is a complete, continuous layer of muscular fibres which have a circular arrangement, *i.e.*, are arranged in a ring-like manner around the long axis of the body; while the inner layer is not continuous, consisting, in fact, merely of five flattened bands which run longitudinally from the oral to the anal extremities, each underlying one of the ambulacral areas. In close contact with each of these bands, on its inner surface, runs a *radial ambulacral vessel* (Fig. 716, *rad. amb.*) together with a *radial nerve*.

Ambulacral System.—Just behind the bases of the tentacles, and surrounding the beginning of the œsophagus, is a *circular ambulacral vessel* (*ring-ves.*) which gives off the five *radial vessels*; these first run forwards and give off branches to the tentacles, and then backwards, passing along the ambulacral areas and giving off branches to the tube-feet, each of which is provided with its *ampulla*. From the ring-vessel also arises a large pear-shaped *Polian vesicle* (*pol. ves.*), and one or more short sinuous canals, the *madreporic canals* (*mad. can.*), which end in a perforated extremity—not situated, like the madreporite of the Starfish or Sea-urchin, on the outer surface of the body, but in the interior of the cœlome.

A **nerve-ring** surrounds the mouth and gives off the five *radial nerves*.

Both **perihæmal** and **hæmal** systems are well developed. The latter comprises a ring-like strand (*ri. bl. ves.*) situated close to the nerve-ring and sending off five radial strands, as well as dorsal and ventral strands (*int. ves.*)

accompanying the enteric canal, and a plexus surrounding the left *respiratory tree* (p. 714).

The **cœlome** contains a fluid in which float numerous amœbocytes, similar

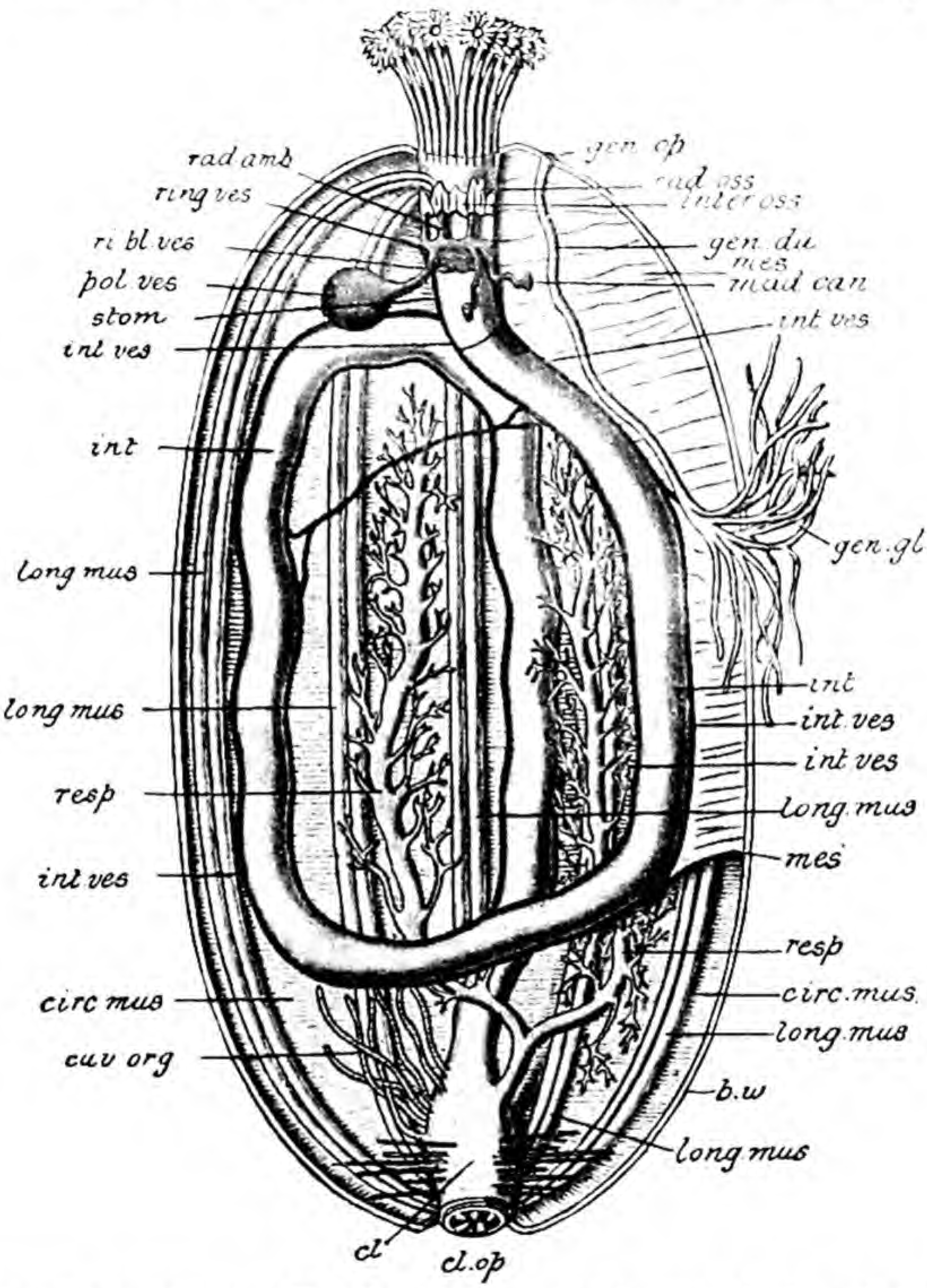


FIG. 716.—Internal organs of a **Holothurian** as seen when the body-wall is divided along the middle of the dorsal surface. *b. w.* body-wall; *circ. mus.* circular layer of muscle; *cl.* cloaca; *cl. op.* cloacal opening; *cuv. org.* Cuvierian organs; *gen. op.* genital aperture; *gen. du.* genital duct; *gen. gl.* gonad; *int.* intestine; *inter. oss.* inter-ambulacral ossicles; *int. ves.* intestinal hæmal strands; *long. mus.* longitudinal band of muscle; *mad. can.* madreporic canal; *mes.* mesentery; *pol. ves.* Polian vesicle; *rad. amb.* radial ambulacral vessel; *rad. oss.* ambulacral ossicles; *ri. bl. ves.* ring strand of hæmal system; *resp.* respiratory trees; *ring-ves.* ring-vessel of the ambulacral system; *stom.* stomach. (After Leuckart.)

to those of the Starfish, and also a number of flattened nucleated corpuscles containing a red colouring matter—said to be hæmoglobin.

The **enteric canal** is, as already mentioned, surrounded at its oral extremity by the circlet of *tentacles*, and within these, when they are fully exserted, is a

narrow *peristome* with the mouth in the centre. When the tentacles are retracted the peristome becomes inverted, so that peristome and tentacles are enclosed within a chamber, the *buccal chamber*, into which the mouth leads. Surrounding the *œsophagus*, which lies immediately behind the buccal chamber, is a circlet of ten *circum-œsophageal ossicles*, five ambulacral (*rad. oss.*) in position, and five inter-ambulacral (*inter. oss.*). Through each of the former pass the corresponding radial ambulacral vessel, hæmal strand, and nerve. The alimentary canal itself is a simple cylindrical tube, only indistinctly marked out into œsophagus, stomach (*stom.*), and intestine. It forms several coils within the cœlome, to the wall of which it is attached by a thin membranous dorsal mesentery, and terminates behind in a comparatively wide chamber, the *cloaca* (*cl.*).

Opening into the cloaca is a pair of so-called *respiratory trees* (*resp.*). Each of these, beginning behind in a single tubular stem, becomes elaborately branched in front, some of the branches reaching nearly to the anterior end of the body-cavity. Each of the terminal branches ends in a small enlargement or ampulla.

Reproductive Organs.—The Sea-cucumber, like the Starfish and Sea-urchin, has the sexes separate. *Ovaries* and *testes* (*gen. gl.*) are very like one another, and consist of bunches of tubular follicles, which communicate with the exterior by means of a duct opening on the dorsal surface some little distance behind the oral end (*gen. ap.*).

The early stages of **development** are very similar to those of the Starfish (p. 698). The bilateral larva, however, assumes a shape and an internal structure which is different from that of the Asteroidea; it is termed the *auricularia* (Fig. 730): it has a number of short processes developed in the course of the ciliated bands. The larval mouth and œsophagus, instead of being abolished as in the case of the Starfish, persist to the adult condition.

4. Example of the Crinoidea.

A Feather-star.—*Antedon rosacea.*

General External Features.—In the Feather-star (Fig. 717), as in the Starfish, there are to be recognized a central disc and a series of five radiating arms. In the natural position of the animal the side of the disc which corresponds to the oral or actinal surface of the Starfish is directed *upwards*, and the aboral or abactinal surface *downwards*. The five arms are bifurcated at their bases; they are feather-like and highly flexible, acting as the locomotive organs of the animal, their alternate flexions and extensions resulting in a slow movement through the water. On the aboral side of the disc are whorls of slender, curved, cylindrical appendages, the *cirri* (Fig. 718), by means of which the Feather-star is enabled to anchor itself temporarily to a rock or a sea-weed.

On the oral side of the disc the body-wall is soft and flexible, containing only scattered irregular spicules of calcareous matter; and in the centre of this surface is an opening, the *mouth* (Fig. 719, *mo.*). From the mouth five very

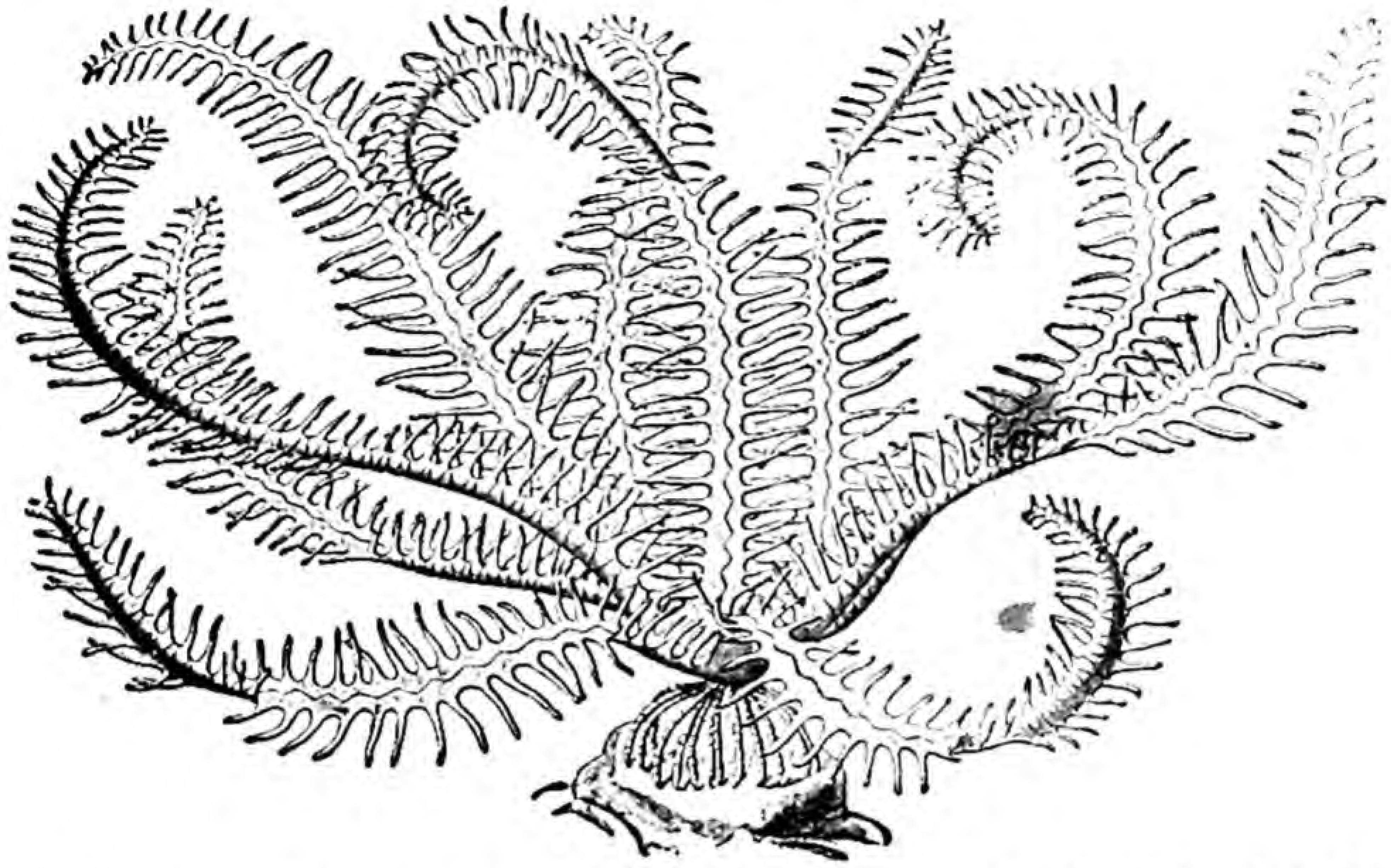


FIG. 717.—**Antedon.** Side view of entire animal. (From Leuckart and Nitsche's Diagrams.)

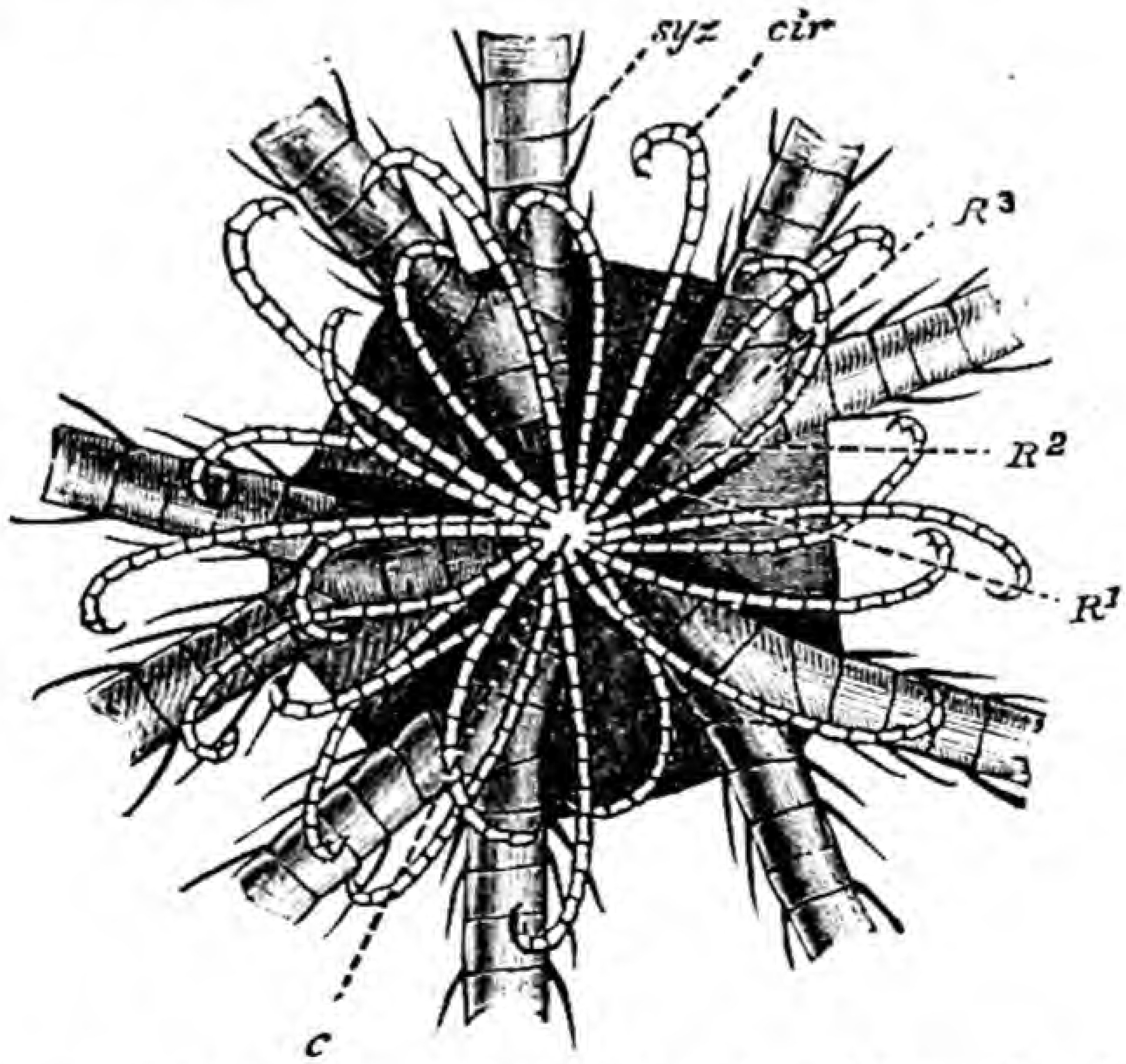


FIG. 718.—Aboral view of **Antedon.** *c.* centrodorsal ossicle; *cir.* cirrus; R^1, R^2, R^3, the three radial plates of one column; *syz.* syzygy or articulation. (After MacBride.)

narrow ciliated grooves, the *ambulacral* or *food-grooves*, radiate outwards towards the bases of the arms, near which they bifurcate, so that ten grooves are formed, one passing along the oral surface of each of the ten arm-branches

to its extremity. The *anal opening* (*an.*) is likewise on the oral surface, being situated on a papilliform elevation in the interspace between two of the radiating canals.

The aboral side of the disc is occupied by a large, flat, pentagonal ossicle, the *centro-dorsal ossicle* (Fig. 718, *c.*; and Fig. 721, *CD*), bearing on its outer surface a number of little cup-like depressions, with which the bases of the cirri are connected. The cirri (*cirr.*) consist each of a row of slender ossicles, covered, like all the rest of the animal, with epidermis, and connected together by means of muscular fibres. Concealed from view by the centro-dorsal ossicle is a thin plate termed the "*rosette*" (Fig. 721, *ros.*), formed by the coalescence of the *basals* of the larva. At the sides are five *first radial ossicles* (R^1), also partly concealed by the centro-dorsal ossicle: with each of these articulates a *second radial* (R^2), which is visible beyond the centro-dorsal. With each of the second radials articulate two *third radials* (R^3), each forming the base of the corresponding arm-branch.

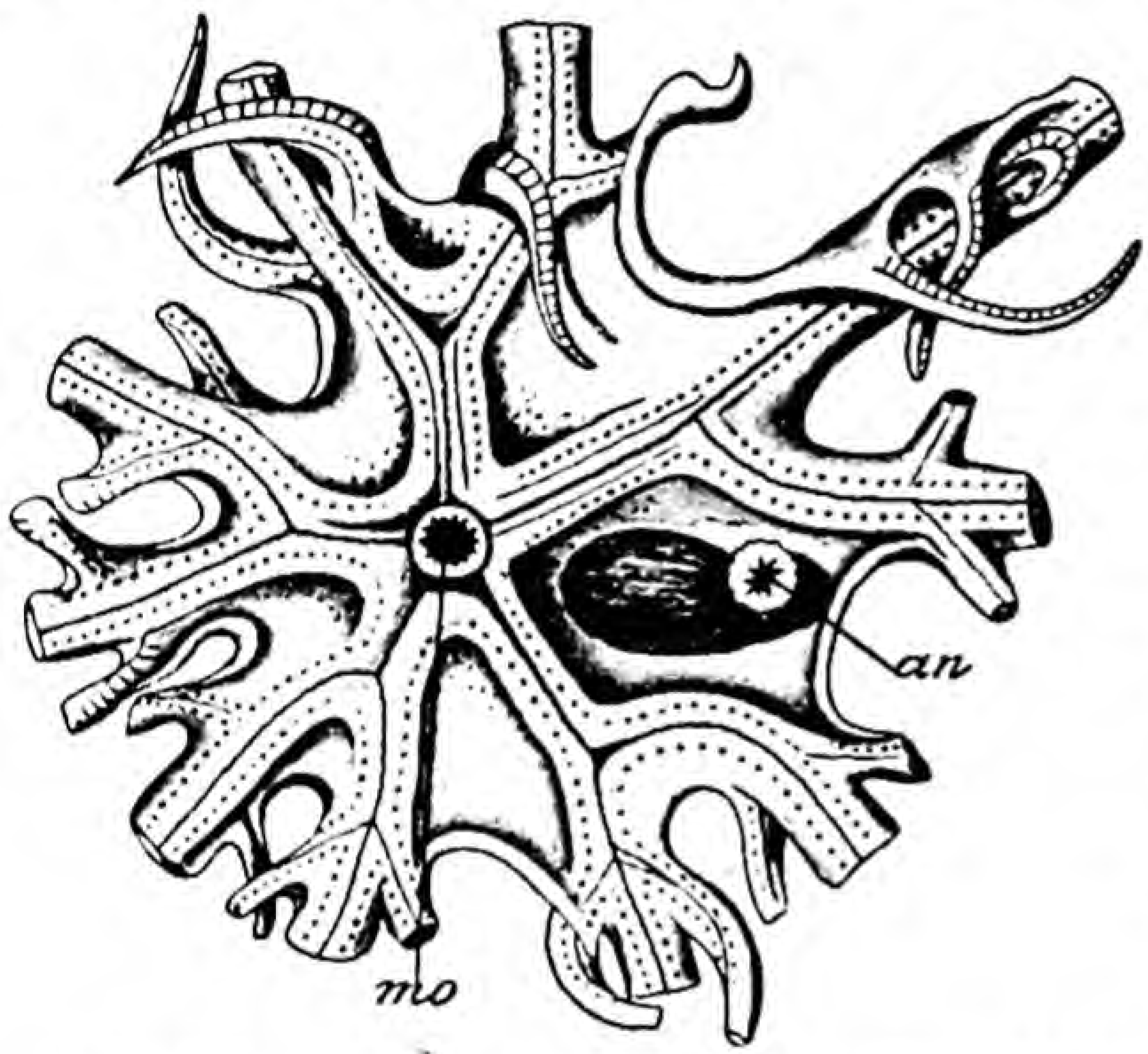


FIG. 719.—**Antedon**, oral (upper) surface of the central disc. *an.* anus; *mo.* mouth. (From Vogt and Jung.)

The ossicles of the arms—*brachials* ($Br.^1$, $Br.^2$)—are arranged in a single row in each arm. They are somewhat elongated in the direction of the long axis of the arm, strongly convex on their aboral surfaces, longitudinally grooved on the oral surface, and connected together by the investing epidermis and by bundles of muscular fibres, by the contractions of which the movements of the arms are brought about. Fringing the sides of each arm are two rows of side-branches, or *pinnules*, each supported by its row of connected ossicles, and each grooved along its oral surface.

The **cœlome** contains numerous strands of connective-tissue which serve to suspend the various organs.

Extending through the arms and pinnules between the supporting ossicles and the ambulacral grooves are three canals, ciliated in parts, which are prolongations of the cœlome (Fig. 720, *cœl. can.*). Two of these—the *sub-tentacular canals*—form a pair separated from one another by a median septum underlying the ambulacral groove. The other—the *cœliac canal*—runs between these and the supporting ossicles (*oss.*). The sub-tentacular canals and the cœliac canal communicate with one another at the extremity of each pinnule.

The **enteric canal** begins with a wide, funnel-shaped *œsophagus* leading to a spacious *stomach* which gives off a number of short, blunt, diverticula and a pair of longer, narrower, " hepatic " cæca, which are slightly branched at the ends. Distally the stomach becomes contracted and opens into a wide *intestine*, which winds round the cœlome, becoming narrower where it passes upwards to open on the exterior, the terminal part, or *rectum*, projecting as a tubular papilla on the surface. In the living animal the rectal tube is observed to undergo frequent movements of contraction and dilatation, by means of which water is drawn into and expelled from the intestine; so that here, as in the Sea-urchin, there would appear to be a process of intestinal respiration.

The **ambulacral system** consists of a *ring-vessel* surrounding the mouth, and a series of *radial vessels* (Fig. 720, *rad. amb.*) which run in the ambulacral grooves, giving off branches to the pinnules. Connected with the radial vessels and their branches is a series of minute tubular ciliated appendages, the *podia* or so-called *tentacles* (Fig. 721, *tent.*), which are homologous with the tube-feet of the Starfishes and Sea-urchins, but are devoid of terminal suckers. These are not organs of locomotion: they bear numerous sensory papillæ, and are therefore to be looked upon as tactile organs, but they probably also have a respiratory function. Connected with the ring-vessel are a number of ciliated tubular diverticula, the *water-tubes*, which are suspended within the cœlome, and open freely into it at their extremities. A large number of vessels with minute ciliated openings—the *water-pores* (*wat. p.*)—lead through the actinal wall of the disc: these and the ciliated tubes are to be considered as together representing the madreporic canal and its openings in the Starfish and Sea-urchin.

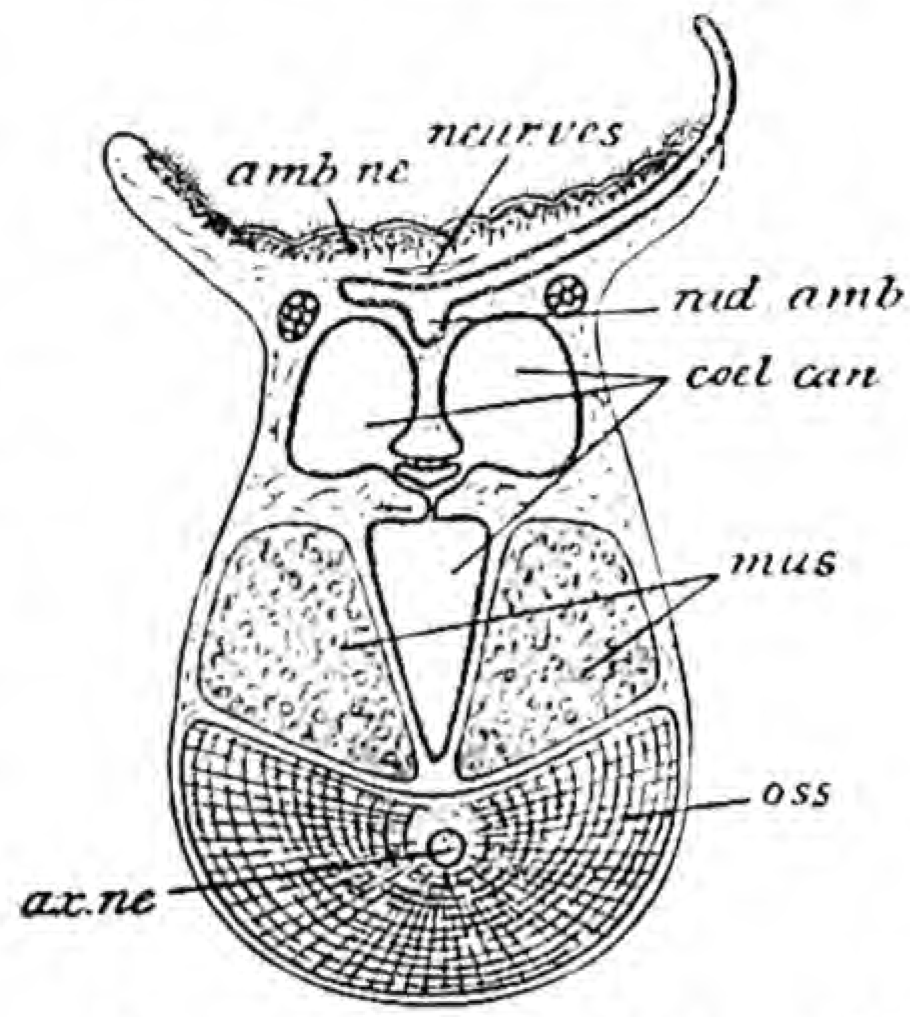


FIG. 720.—**Antedon,** transverse section of a pinnule. *amb. ne.* radial nerve of the superficial (ambulacral) nervous system; *ax. ne.* axial nerve; *cœl. can.* sub-tentacular and cœliac canals; *mus.* muscles; *neur. ves.* radial sinus of the perihæmal system; *rad. amb.* radial ambulacral vessel giving off branches to the tentacles. Between the paired sub-tentacular and unpaired cœliac canals is the genital rachis. The small round bodies above the line from *rad. amb.* are the sacculi. (After Teuscher.)

The **nervous system** consists of two perfectly distinct parts—*superficial* and *axial* or *aboral.* A superficial radial nerve-ring (*ect. ne.*) surrounds the mouth, and from it are given off a series of nerves—thickenings of the epidermis of the ambulacral grooves and their offsets—which extend throughout the length of the arms and pinnules. In the axis of the supporting ossicles of the arm is an *axial nerve* (*ax. co.*), which gives off branches (Fig. 720, *ax. ne.*) running through the axes of the ossicles of the pinnules. The axial nerves are con-

nected internally, not with the circum-oral nerve-ring, but with a central body situated below the rosette, in the interior of the centro-dorsal ossicle. This, the *central capsule* (Fig. 721, *cent. caps.*), forms the investment of a body termed the *five-chambered organ* (*chamb. org.*) divided into five parts by radial septa, and continuous with the aboral end of the genital stolon. Processes from the five angles of the central capsule combine to form a pentagonal ring from which pass outwards the axial nerves of the arms. This system controls the movements of the arms. Aborally the central capsule gives off nerves to the cirri.

A system corresponding to the **perihæmal system** of the Starfish is present, though reduced, and there is a highly-developed and complicated **lacunar** or **hæmal system.**

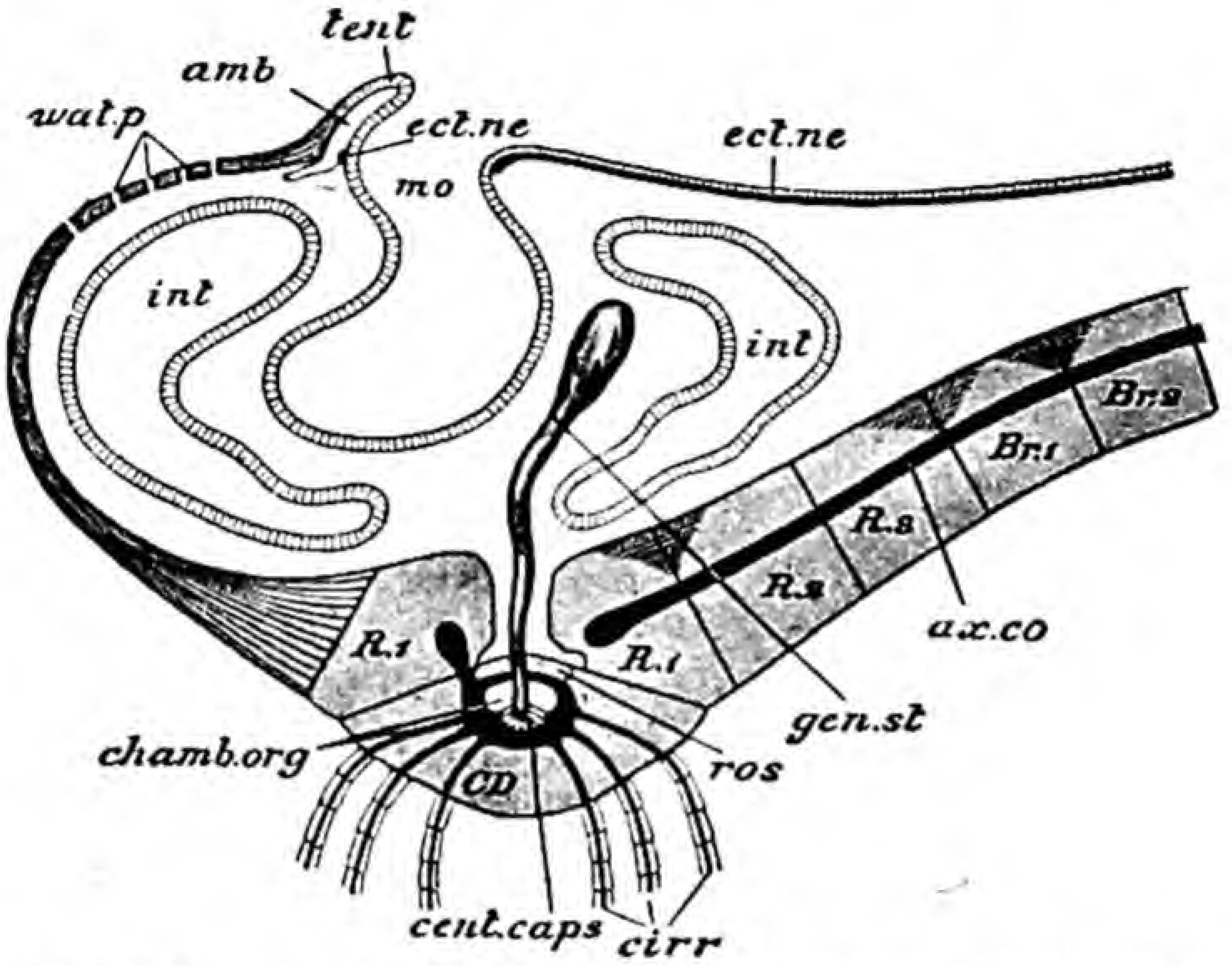


FIG. 721.—**Antedon.** Diagrammatic view of a median vertical section through the disc, passing through one radius and one inter-radius. *amb.* ambulacral vessels; *ax. co.* axial nerve-cord passing through the ossicles of the arm; *Br.*^{1} Br.^{2} brachial ossicles; *CD.* centro-dorsal ossicle; *cent. caps.* central capsule; *chamb. org.* chambered organ; *cirr.* cirri; *ect. ne.* ambulacral (epidermal) nerve-ring and radial nerve; *gen. st.* genital stolon; *int.* intestine; *mo.* mouth; *R.*^{1}, *R.*^{2}, *R.*^{3} radials; *ros.* rosette; *tent.* tentacles; *wat. p.* water-pores. (After Milnes Marshall.)

Numerous bodies termed the **sacculi**, the character of which has given rise to much discussion, occur regularly arranged along the ambulacral grooves and also in other parts. These are small spherical bodies which become vividly coloured when treated with staining agents. They are essentially collections of amœboid cells which may represent reserve materials, stored up for the nutrition of the animal, or may contain excretory matters.

The **reproductive organs**—*ovaries* or *testes*, as the case may be—are lodged in the dilated bases of the pinnules, which become considerably enlarged as the ova or sperms mature, those next to the bases of the arms alone remaining sterile. When mature, the sexual elements escape by means of short ducts. Each gonad is one of the terminal parts of a system of cords of cells enclosed in narrow tubes extending from a central part or *genital stolon* (*gen. st.*)—connected

dorsally with the chambered organ—outwards through the arms; the terminal portions, lying in the pinnules, are dilated to form the reproductive organs, and the cells of their epithelium become developed into ova or sperms, while the rest constitute a non-fertile connecting rachis. This system is enclosed throughout by a plexus of hæmal lacunæ.

Like the rest of the Echinoderms, the Feather-star undergoes a *metamorphosis* (Figs. 731 and 732). It passes through a free-swimming ciliated larval stage, which is followed by a fixed stalked stage known as the "*pentacrinoid*" larva on account of the resemblance which it bears to the adult *Pentacrinus*, one of the permanently fixed members of the same class. This fixed pentacrinoid larva passes into the adult free-swimming Feather-star by the development of the dorsal cirri, the elongation of the arms, and the absorption of the stalk.

5. Distinctive Characters and Classification.

The Echinodermata are radially symmetrical animals, the radial arrangement of whose parts imperfectly conceals a fundamental bilateral symmetry. The surface is covered with an exoskeleton of calcareous plates or ossicles, which usually support a system of movable or immovable calcareous spines. There is a large body-cavity or cœlome, and well-developed alimentary, nervous, and vascular systems. A characteristic system of vessels, the ambulacral system, is connected with the locomotion of the animal, as well as with other functions: the organs of locomotion are in most cases elastic and contractile tubular bodies, the tube-feet, which are appendages of the ambulacral system. Nearly all the systems of organs of the animal partake to a greater or less extent of the general radial form of the body. Reproduction is entirely sexual. In the course of its development from the egg the Echinoderm passes through a peculiar larval stage, in which the symmetry of parts is bilateral, instead of radial as in the adult animal. All the Echinodermata are marine.

The Echinodermata are classified as follows:—

SUB-PHYLUM I.—ELEUTHEROZOA.

Echinodermata devoid of a stalk, and always freely locomotive in the adult condition: with a system of radial ambulacra in the form of grooves or areas radiating out from the mouth, and containing a double series of tubular appendages of the ambulacral system, the tube-feet, usually employed in locomotion, and in the majority of cases provided with terminal suckers: the anus usually aboral; the mouth on the surface that is habitually directed downwards, or at the end habitually directed forwards in locomotion.

CLASS I.—ASTEROIDEA.

Eleutherozoa with star-shaped or pentagonal body, in which a central disc and usually five arms are more or less readily distinguishable, the arms

being hollow, and each containing a prolongation of the cœlome and of its contained organs. There are distinct oral and aboral surfaces, on the former of which the anus and the madreporite are situated, and on the latter the mouth and five narrow ambulacral grooves lodging the tube-feet. The larva has the form either of a *bipinnaria* or of a *brachiolaria*. This class includes the Starfishes.

ORDER 1.—PHANEROZONIA.

Asteroidea in which there are large marginal plates round the margin of arms and disc. The dermal branchiæ are limited to the aboral surface. This order includes *Anthenea* (Fig. 722), *Asterina*, *Astropecten*, *Pentaceros*, and others.

ORDER 2.—CRYPTOZONIA.

Asteroidea in which the marginal plates are small or absent; the dermal branchiæ are not limited to the aboral surface. This order includes *Asterias* (Fig. 689), *Solaster*, the deep-sea Asteroid *Brisinga*, and others.

CLASS II.—OPHIUROIDEA.

Star-shaped Eleutherozoa, with a central disc and usually five arms, which are more sharply marked off from the disc than in the Asteroidea and which contain no spacious prolongations of the cœlome. There are distinct oral and aboral surfaces. The anus is absent; the mouth, as well as the madreporite, on the oral surface. Except in one fossil order there are no ambulacral grooves. The larva is a *pluteus*. This class includes the Sand-stars and Brittle-stars.

ORDER 1.—LYSOPHIURÆ.

Extinct Ophiuroids with ambulacral grooves.
Silurian and Devonian.

ORDER 2.—STREPTOPHIURÆ.

Ophiuroids in which the ambulacral ossicles articulate with one another by simple ball-and-socket joints.

ORDER 3.—CLADOPHIURÆ.

Ophiuroids in which the ambulacral ossicles articulate with one another by means of hour-glass-shaped surfaces. The arms may be branched. This order includes *Astrophyton* (Fig. 724), *Euryale*, and others.

ORDER 4.—ZYGOPHIURÆ.

Ophiuroids in which the movement of the ambulacral ossicles on one another is restricted by the presence of lateral processes and pits. This order includes *Amphiura*, *Ophioglypha* (Fig. 723), and others.

CLASS III.—ECHINOIDEA.

Eleutherozoa with globular, heart-shaped, or disc-shaped body enclosed in a shell or corona of close-fitting, firmly united calcareous plates. The mouth is nearly always polar; the anus usually at the opposite (aboral) pole; the madreporite is close to the latter. There are no ambulacral grooves; but the surface is divided into alternating ambulacral and inter-ambulacral zones or areas, which usually run from pole to pole. The larva is a *pluteus*. This class includes the Sea-urchins, with the Heart-urchins and Cake-urchins.

ORDER 1.—REGULARIA.

Echinoidea with globular corona containing, in most cases, twenty meridional rows of plates. Mouth and anus polar. A lantern of Aristotle is present. This order includes the Sea-urchins: *Asthenosoma*, *Cidaris*, *Arbacia*, *Echinus* (Figs. 708, 710), *Strongylocentrotus* (Fig. 709), and others.

ORDER 2.—CLYPEASTRIDEA.

Echinoidea with more or less flattened corona, with the mouth central the anus excentric. A lantern of Aristotle is present. This order includes the Cake-urchins (*Clypeaster*, Fig. 728).

ORDER 3.—SPATANGOIDEA.

Heart-shaped Echinoidea with the mouth and anus excentric. No lantern of Aristotle. This order includes the Heart-urchins: *Hemipneustes* (Fig. 727), *Spatangus*, *Echinocardium*, and others.

CLASS IV.—HOLOTHUROIDEA.

Eleutherozoa with elongated, cylindrical or five-sided body, having the mouth and anus at opposite extremities. The body-wall is usually only supported by scattered ossicles or spicules. There is no external opening to the madreporic canal (except in some *Elasipoda*). The surface usually exhibits five ambulacral areas; but these may be absent. There is a circlet of large oral tentacles. The larva is an *auricularia*. This class includes the Sea-cucumbers and "Bêche-de-mer."

ORDER 1.—ASPIDOCHIROTÆ.

Holothuroidea with tube-feet; with tentacle-ampullæ; tentacles shield-shaped; without retractor muscles; respiratory trees present; madreporite internal. This order includes *Holothuria* (Fig. 716) and others.

ORDER 2.—ELASIPODA.

Deep-sea Holothuroidea with tube-feet; body generally flat ventrally; tentacles shield-shaped; no tentacle-ampullæ; no retractor muscles; no respiratory trees; madreporite internal or external. This order includes *Deima* and others.

ORDER 3.—PELAGOTHURIDA.

Pelagic Holothuroidea differing from the Elasipoda by the absence of tube-feet and the presence of large tentacle-ampullæ. This order includes *Pelagothuria* and others.

ORDER 4.—DENDROCHIROTÆ.

Holothuroidea with tube-feet, retractor muscles, and respiratory trees; tentacles arborescent; tentacle-ampullæ absent; madreporite internal. This order includes *Cucumaria, Colochirus, Psolus*, and others.

ORDER 5.—MOLPADIDA.

Burrowing Holothuroidea without tube-feet; tentacles unbranched or dinnate; with respiratory trees; with tentacle-ampullæ, and sometimes with retractor muscles; madreporite internal. This order includes *Caudina, Molpadia*, and others.

ORDER 6.—SYNAPTIDA.

Burrowing Holothuroidea without tube-feet and without radial ambulacral vessels; without respiratory trees; tentacles pinnate with vestigial ampullæ; retractor muscles present; madreporite internal. This order includes *Sinapta, Rhabdomolgus*, and others.

SUB-PHYLUM II.—PELMATOZOA.

Echinodermata which are usually fixed at the base, and usually supported on a stalk composed of a row or rows of ossicles (Fig. 729): the mouth on the free surface, near or in the centre, and having extending out from it on the oral surface a radially arranged system of narrow, ciliated ambulacral grooves, having the function of food-grooves, which may run between the plates of the theca, on the surface of the theca, or along the oral surfaces of a system of radial processes or arms given off from it. The tube-feet of other Echinoderms, when represented, take the form of small, tubular, strongly ciliated appendages (tentacles) without suckers: the anus usually on the oral surface.

CLASS I.—CRINOIDEA.

Mostly fixed, stalked Pelmatozoa in which there is a theca comprising five regularly arranged radial and five basal plates, giving off five, usually branched, joined processes or arms; with food-grooves radiating out from the mouth

along the oral surfaces of the arms, and extending along their branches: the central parts of the ambulacral, nervous, and reproductive systems, and of the cœlome, lodged in the theca, send extensions through the arms.

This class comprises, together with many extinct forms, the only living Pelmatozoa.

Order 1.—Monocyclica.

Crinoidea in which the base of the theca comprises basals only.

Order 2.—Dicyclica.

Crinoidea in which the base comprises basals and infra-basals. This order includes *Metacrinus* (Fig. 729), *Antedon* (Fig. 717), *Comatula* (*Actinometra*), and others.

CLASS II.—CYSTOIDEA.

Fixed, stalked, or sessile Pelmatozoa, with the plates of the theca sometimes irregular, sometimes arranged in a regular radial system, with food-grooves extending for a longer or shorter distance over the surface of the theca, sometimes on special plates lying above those of the latter, their terminal parts extending on to a varying number of unbranched arms or "fingers"; the theca perforated completely or partially by numerous pores which are supposed to have lodged respiratory processes.

Lower Silurian to Carboniferous.

CLASS III.—BLASTOIDEA.

Fixed Pelmatozoa with well-developed stalk, and theca with a regular system of plates; with five, rarely four, food-grooves radiating out from the central mouth, and each borne on a special "lancet plate," the inter-radial intervals between which are occupied by a corresponding number of oral or "deltoid" plates. The grooves are bordered by a series of side plates bearing small branches or "fingers" to which side branches of the grooves extend. In the intervals between the grooves on the aboral sides of the deltoids are a whorl of plates perforated by the apertures of groups of internally situated respiratory folds (*hydrospires*). The anus is eccentrically situated on the oral surface.

Upper Silurian to Carboniferous.

CLASS IV.—EDRIASTEROIDEA.

Fixed (or sometimes free?) Pelmatozoa, usually sessile, rarely with a short stalk; with sac-like, cushion-shaped or disc-shaped theca made up of numerous plates devoid of any regular arrangement and without any appendages; with central mouth and five straight or curved radiating food-grooves bordered by covering plates: anus and madreporite on oral side.

Cambrian to Carboniferous.

6. General Organization.

General Form and Symmetry.—Like the Cœlenterata, the Echinodermata are radially symmetrical, the body being capable of division into a series of sub-equal *antimeres* along a series of radiating planes at right angles to the principal axis. In the majority of existing forms (Asteroidea, Ophiuroidea and Crinoidea) the radial symmetry is expressed in the external form of the body, which is produced into a number of radially disposed parts, the *arms* or *rays*, arranged around a smaller or larger *central disc*. But in the Echinoidea the body is sub-spherical, and in the Holothuroidea sub-cylindrical, the radiate arrangement being in these classes indicated externally only by the distribution of the podia, and internally by that of certain of the systems of organs.

Although, however, the general external form and the arrangement of some of the internal organs in the Echinodermata indicates a radial symmetry, it is invariably found that this radial arrangement serves to hide a *bilateral* symmetry which is more primitive. This is best marked in the larva, which has pronounced bilateral instead of radial symmetry, but is quite recognizable in the adult. In all Echinoderms there is, passing through the primary axis, a plane—the *median* plane—along which, and along which alone, the body is capable of being divided into two equal—or, to speak more correctly, approximately equal—right and left halves. The existence of such a single median plane is, as already explained, indicative of the bilateral form of symmetry.

The body is most usually five-rayed (Ophiuroidea, most Asteroidea, Crinoidea), cylindrical (most Holothuroidea), or globular (most Echinoidea), the surface in the two last cases being marked by five bands or zones of tube-feet, which divide it into five *ambulacral* and five *inter-ambulacral* areas. In the Ophiuroidea and Asteroidea two of the rays—constituting the *bivium*—have between them the *madreporite*, marking the position of the madreporic canal of the ambulacral system; the remaining three rays form the *trivium*. The median plane passes through the madreporite, and thus midway between the two rays of the bivium, and bisects longitudinally the middle ray of the trivium. A corresponding disposition of the parts is traceable also, as will be subsequently shown, in the cylindrical and globular Echinoderms.

In all the Echinodermata aboral or abactinal and oral or actinal surfaces are more or less distinctly recognizable. In the Asteroidea, Ophiuroidea, and Echinoidea, the actinal surface is that in the middle of which the mouth is situated, and which is, in the natural position of the animal, directed downwards or towards the surface to which it is clinging. The opposite abactinal surface is, in the majority of the Asteroidea and Echinoidea, marked by the presence of the anal aperture: in the Ophiuroidea and some Asteroidea the anus is absent; in some Echinoidea it is situated on the border between the two surfaces, or even on the oral surface. In the Crinoidea the oral surface,

which is habitually directed upwards in the natural position of the animal bears both mouth and anus, the former central, the latter eccentric and inter-radial. In the fixed Crinoids the abactinal or aboral surface has attached to its centre the distal end of the stalk; in the free forms it has connected with it whorls of slender curved appendages, the *dorsal cirri*, by means of which temporary attachment is effected. In the Holothurians, owing to the elongation of the body in the direction of the line joining mouth and anus, oral and aboral surfaces corresponding to those of the other classes are not distinguishable; but in many, as for example in *Colochirus*, there is a marked difference between one surface—the *dorsal*, which is habitually directed upwards, and another—the *ventral*, which is habitually directed downwards.

In considering the general external form in the various classes of Echinoderms, we have to take into account the arrangement of the *tube-feet*—the organs of locomotion—as these have important relations to the other parts and to the whole plan of organization of the animal. These organs, as previously explained, are tubular appendages with highly elastic and contractile muscular walls, capable of being stretched out so as to extend a long way from the surface of the body. In the majority of cases the tube-foot has at its extremity a *sucking-disc*, by means of which it can be attached; in a few, however, the sucking-disc is absent.

The *epidermis* is ciliated in all but the Holothuroidea. In the subjacent dermal layers there are always present, except in *Pelagothuria* and *Rhabdomolgus* (Holothuroidea), calcareous bodies or *ossicles*, varying very greatly in form and arrangement in the different groups. Movable or immovable calcareous *spines* or *tubercles* projecting on the surface are very general. Peculiarly modified spines, termed *pedicellariæ*, are commonly, though not universally, present in certain parts in the Echinoidea and Asteroidea. A pedicellaria consists in essence of two or three calcareous jaw-like pieces or valves, movably articulated together, and capable of being separated or approximated by the contraction of bundles of muscular fibres; sometimes there is a long stalk: sometimes (as in the case of *Anthenea*, p. 698) a stalk is absent; during the life jaws or valves keep opening and closing. That such specialized structures have some important function to perform there can be no doubt, but there is some uncertainty as to what their special purpose is. According to some observers, the pedicellariæ of the Sea-urchin have been seen passing from one to another the particles of fæcal matter discharged from the anus, and their function would thus appear to be a cleansing one. On the other hand, it is stated that when a Sea-urchin is attacked the spines may be bent aside from the assailed portion of the surface so as to allow of the pedicellariæ being brought to bear as defensive weapons on the assailant, and from these and other observations that have been recorded, both on Asteroids and on Echinoids, it is concluded that the main function of these appendages is to act as defensive organs. Pedicellariæ are

absent in the Ophiuroids, but in the Euryalida there are peculiar hook-like organs of adhesion, most abundant on the oral surface and towards the extremities of the arms. The *sphæridia*, which have already been referred to as occurring in the Sea-urchin, are only doubtfully to be regarded as modified spines; they are confined to the Echinoidea. Also confined to that class are the *clavulæ*—slender spines covered with strong cilia, which occur in bands (*fascioles*) on the surface of the Spatangoids. Larger spines, resembling the clavulæ in being covered with strong cilia, occur also on the aboral surface in the Clypeastroids and some Asteroids. The currents produced by the action of their cilia serve to keep constantly renewed the water in the neighbourhood of the anus and of the respiratory podia or the papulæ.

There are two principal **systems of plates** to be recognized, an *oral* and an *apical*; the former corresponding with the oral or actinal, and the latter with the aboral or abactinal surface. The former vary considerably in the different classes: the constant elements are five *orals*, which may or may not be recognizable in the adult. The apical system consists (1) of a *central* plate; (2) of five *basals* which are inter-radial in position; (3) of five *radials* which are radial in position. In the Asteroidea (Fig. 707) the radials are late in making their appearance; before they are developed five *terminal* plates have become distinct, one at the end of each rudimentary arm; these are carried outwards by the extension of the arm, and each supports the corresponding tentacle. As a rule these plates of the apical system are only distinct in the young condition. In the Ophiuroidea the arrangement resembles that observable in the Asteroidea. In the Echinoidea (Fig. 710) the basals (*genitals*) are perforated by the ducts of the reproductive organs; the radials (*oculars*) are perforated for the tentacles: the central (*anal*) rarely persists as a single plate in the adult, usually becoming broken up into a number of irregular plates. In the stalked Crinoidea the term central has been applied to a plate which is transformed into the disc of attachment at the base of the stalk, but the correspondence between this and the similarly named plate in the other classes is very doubtful; the ossicles of the stalk intervene between it and the basals. In the free forms the uppermost segment of the larval stalk, uniting with the central and the infra-basals, is transformed into a *centro-dorsal plate*, and the basals nearly always unite into a *rosette-plate*, which is concealed from view by the centro-dorsal and the radials. The apical system of plates is apparently not represented in the Holothuroidea.

Modifications of Form in the Five Classes.—The general shape in the **Asteroidea** is as already pointed out, that of a star. There is a central part, or *central disc*, from which proceeds a system of radially disposed *arms* or *rays*. The central disc and the rays are usually compressed in the vertical direction, as in Anthenea and Asterina, but in some Starfishes the rays are approximately cylindrical; they nearly always taper distally. In the majority of Starfishes, as in the examples described, the arms are five in number, except in malformed

individuals; but in some they are six, in others seven, eight, or more. The proportions borne by the arms to the central disc are subject to considerable variation. In some, as in Asterias, the arms are long, and the central disc appears as little more than their point of union; in others, again, owing to coalescence of the arms, the whole Starfish has the form of a five-sided disc, in which the arms are represented only by the five angles; while between these two extremes there are numerous intermediate gradations. The *Brisingidæ* differ from all the rest of the class in having the arms almost as sharply separated off from the central disc as in the Ophiuroids.

The *abactinal* or *aboral* and the *actinal* or *oral* surfaces are always distinctly marked off from one another. In the middle of the latter (Fig. 722) is the *mouth*, running out from which are five or more narrow *ambulacral grooves*, one of which is continued along the oral surface of each arm to its extremity. Near to, but not quite in, the middle point of the aboral surface is the *anal aperture*, absent in a few instances; and on the same surface, nearer the margin between the two rays of the bivium in the five-rayed Starfishes, is the *madreporite*, a finely grooved calcareous plate perforated by a number of minute apertures. In some fossil Starfishes it is situated on the oral surface. Sometimes instead of one madreporite there are several.

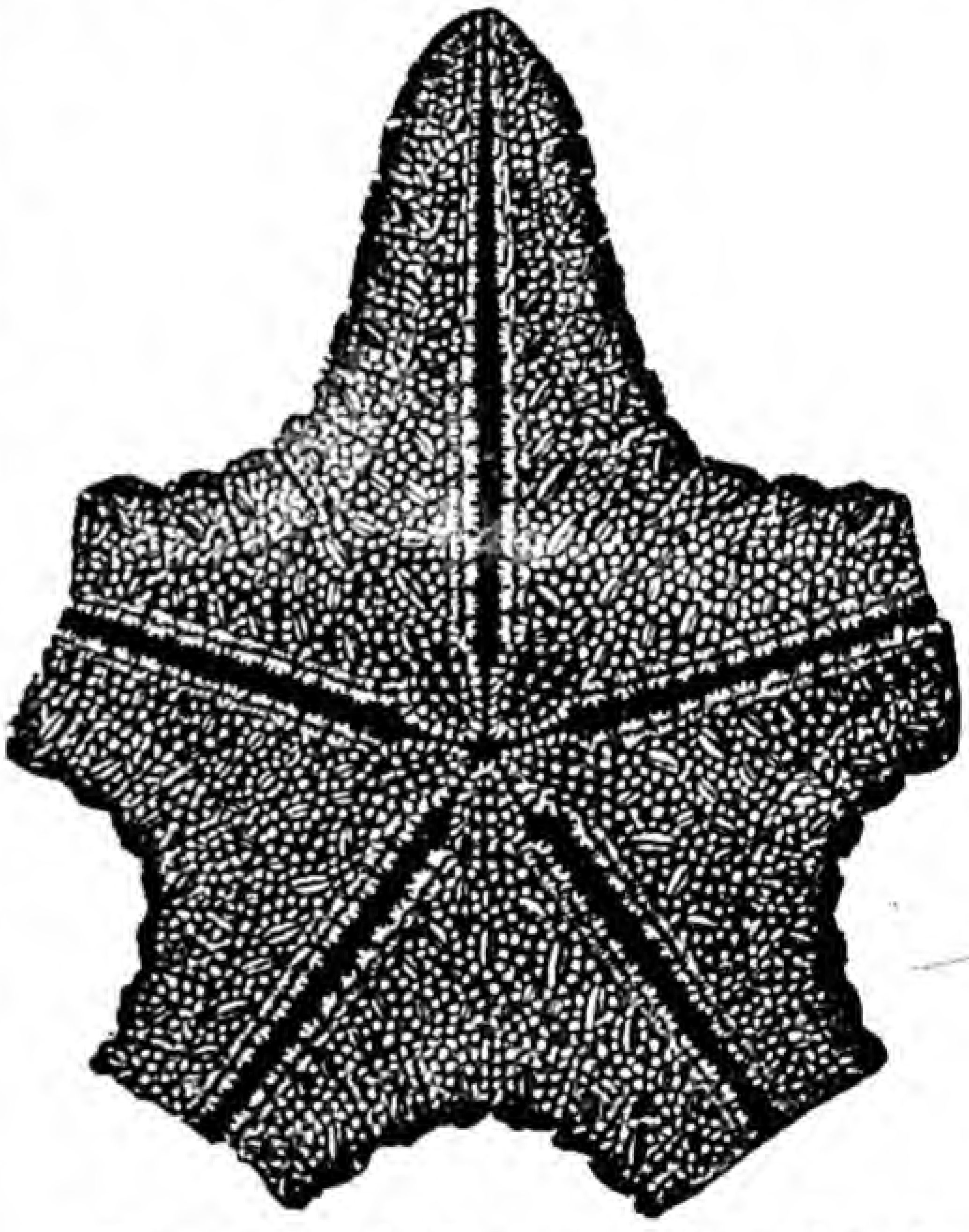


FIG. 722.—**Anthenea.** View of oral surface. (After Sladen.)

The wall of the body in the Starfishes contains a number of calcareous *ossicles*, movably articulated together and connected by bands of muscle, so that, though the body is firm, and in the dried condition often quite rigid, the arms are capable during life of slow movements of flexion and extension, enabling the animal to creep through comparatively small fissures and crannies. A special system of ossicles—the *ambulacral ossicles*—are arranged in a double row along each ambulacral groove, the ossicles of the two rows articulating movably with one another at the apex of the groove. At the end of the arm the two rows of ambulacral ossicles end in a *terminal* ossicle which supports the unpaired tentacle. *Spines* are invariably present, but are sometimes confined to the margins of the ambulacral grooves, in which position they are movably articulated with the underlying ossicles. *Tubercles* take the place of spines over most of the surface in many forms. In *Astropecten* the ossicles of the aboral surface take the special form to which the term *paxillæ* is applied.

Each paxilla is a plate which is produced into a short rod, divided at its extremity into a number of radiating processes.

The *tube-feet* are arranged in a double row along each of the ambulacral grooves, each connected through an aperture between the ambulacral ossicles with an ampulla, or, exceptionally, with two ampullæ, situated in the cœlome. Each double row of tube-feet terminates at the extremity of the arm in an unpaired appendage, the *tentacle*, which is tactile and olfactory, and not locomotive in function. The tube-feet are provided (except in Astropecten) with terminal suckers.

In the **Ophiuroidea** (Fig. 723) the *central disc* is much more sharply marked

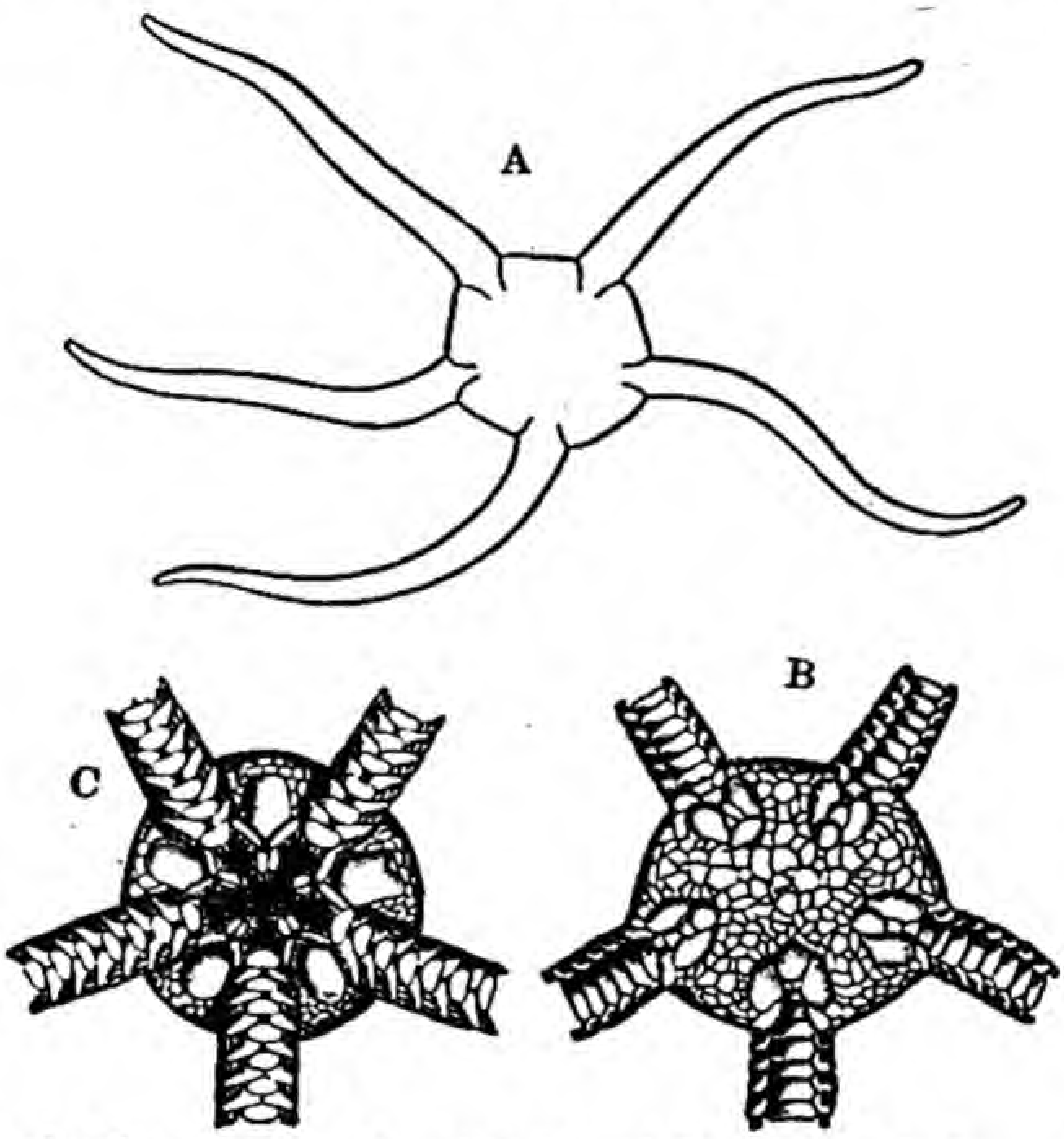


FIG. 723.—**Ophioglypha lacertosa.** *A*, outline, of the natural size. *B*, central disc, aboral surface. *C*, the disc, oral surface showing the mouth and genital fissures. (From Nicholson and Lydekker's *Palæontology*.)

off from the arms than in the Asteroidea. The arms, which are usually five in number, rarely six, are comparatively slender and cylindrical, tapering towards the free extremities ; in one group, the *Euryalida* (Fig. 724), they are branched. The mouth is in the middle of the oral surface of the disc, as in the Asteroidea, but there are no ambulacral grooves, and there is no anal aperture. Five pairs of slits on the oral surface (Fig. 723 *C*) lead into the genital bursæ, which receive the sperms and ova from the gonads, and which appear also to act as organs of respiration and perhaps also of excretion. The surface is covered with thin plate-like ossicles, usually beset along their edges with longer or shorter spines ; sometimes irregular calcareous granules take the place of plates. Hook-like organs of adhesion are present only in the *Euryalida*. Each of the arms is

supported by a row of internally situated *ambulacral ossicles*. Tube-feet are present and are protruded at the sides of the arms between the lateral plate-like ossicles; but they have no sucking-discs and no ampullæ, and locomotion is effected in the majority of the Ophiuroids by active flexions and extensions of the arms. In one genus there is a pair of fin-like appendages, supported by slender spines, on each joint of the arms. The madreporite is situated inter-

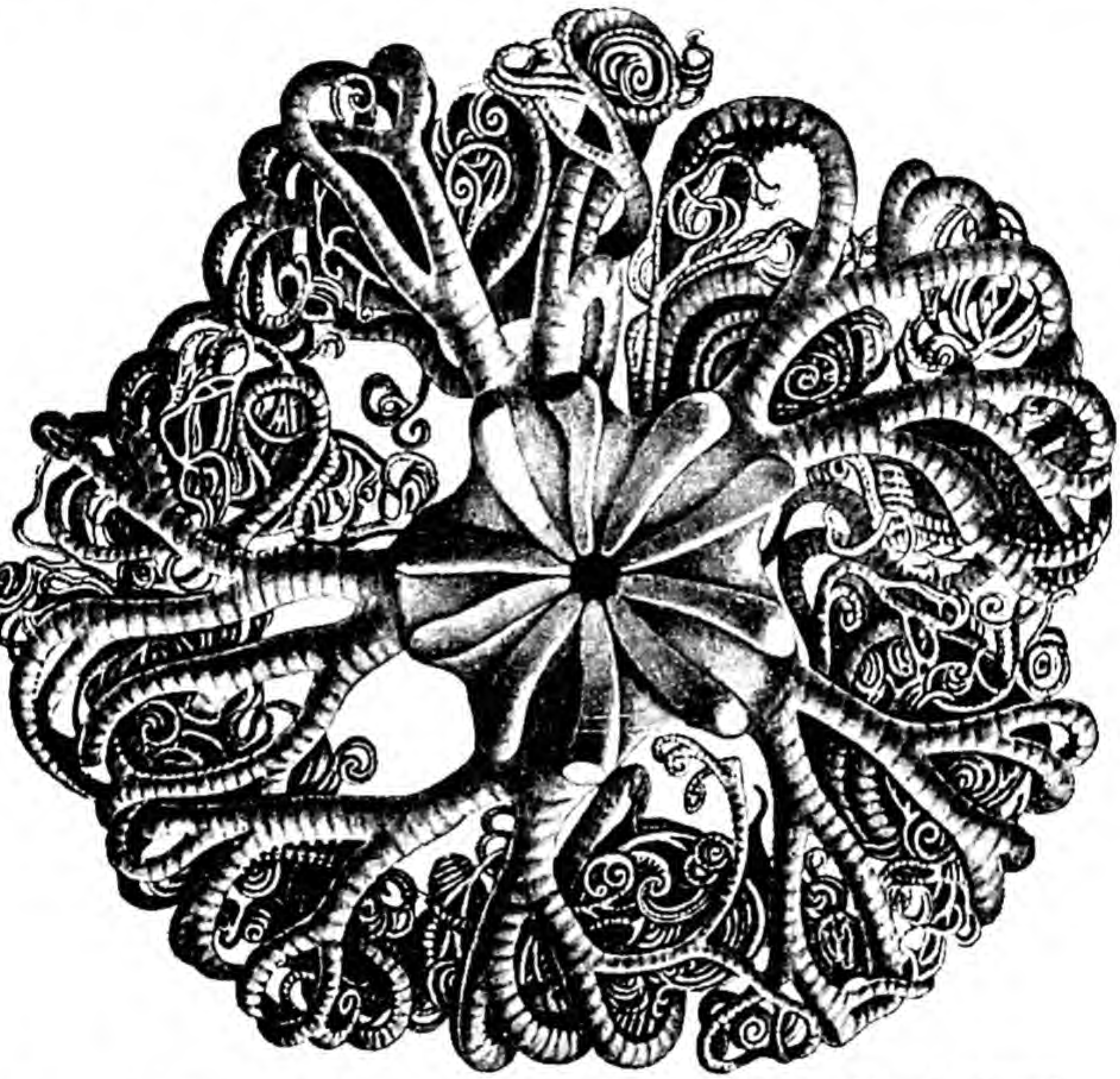


FIG. 724.—**Astrophyton arborescens,** aboral surface. (After Ludwig.)

radially on the oral, and not on the aboral surface as in the Asteroidea. In the Euryalida there are five madreporites and five madreporic canals.

In the **Echinoidea** the body is either globular, or heart-shaped, or flattened and disc-like. The *exoskeleton* is in the form of a rigidly articulated system of calcareous plates, fitting closely together by sutures, so as to form a continuous shell or *corona*. Only *Asthenosoma* and allies, deep-sea forms, differ from all the rest in having a corona possessing a certain degree of flexibility and performing movements which are brought about by the contractions of five longitudinal bands of muscle running along the ambulacral areas on the inner surface.

In the globular forms, or regular Sea-urchins, the mouth is situated at the oral pole of the globe, the anus at the aboral, and the plates of the corona are

in twenty regular meridional rows, arranged in ten zones, five ambulacral and five inter-ambulacral, as described in the account of Echinus, with peristome, periproct, ocular and genital plates, and madreporite. *Spines* (Fig. 725), *pedicellariæ* (Fig. 726), and *sphæridia* are present, as already described (p. 705), the last-named appendages, however, being absent in one group. The spines are usually defensive organs simply, but in some Sea-urchins they act also as the locomotive organs, the animal moving by their agency along the sea-bottom.

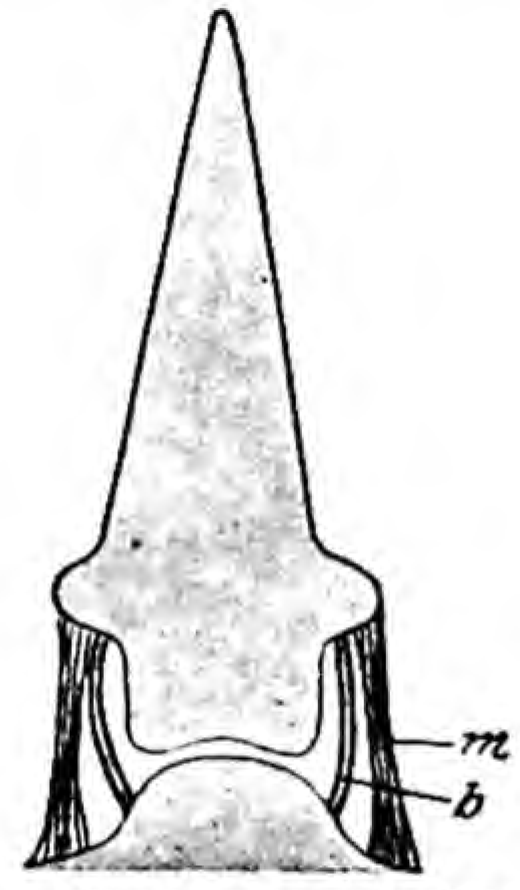


FIG. 725.—Diagram of spine of Sea-urchin, showing mode of articulation. *b*. ligament; *m*. muscle. (From Leuckart.)

FIG. 726.—Pedicellaria of **Arbacia punctulata.** (From Leuckart.)

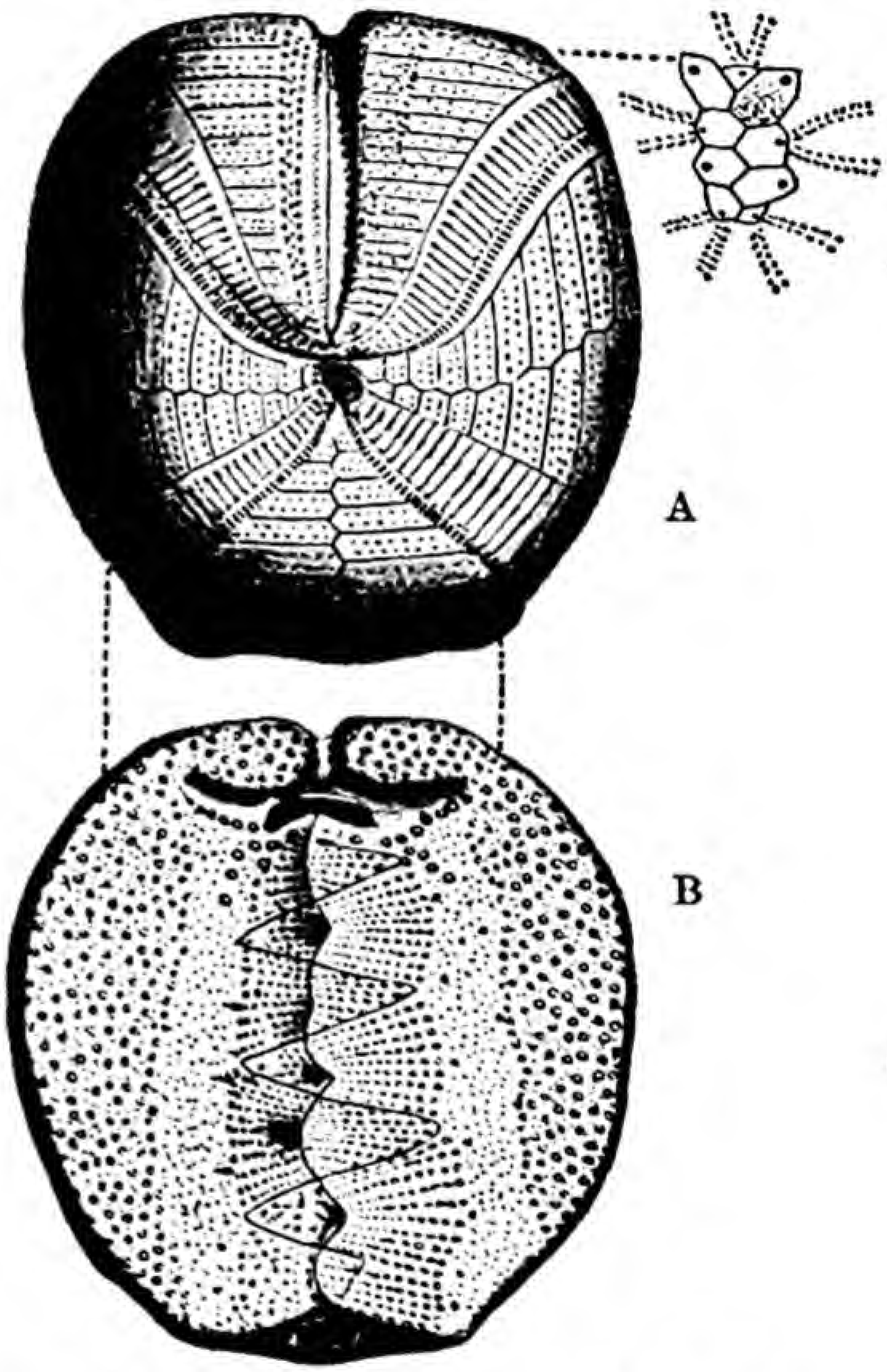


FIG. 727.—**Hemipneustes radiatus.** *A*, aboral, and *B*, oral surface. *C*, apical plates. (From Bronn's *Tierreich.*)

The podia or tube-feet, which are arranged in a double-row in each ambulacral zone, are extremely extensible, and terminate in *sucking-membranes* strengthened by a calcareous *rosette*. An unpaired *tentacle*, corresponding to that of the Asteroidea, is supported on each of the ocular plates at the ends of the ambulacral zones. Two podia in each double row, situated on the peristome, are likewise of the nature of tentacles (*oral* or *buccal tentacles*), and are sometimes devoid of sucking-membranes. Corresponding to the *dermal branchiæ* of the

Asteroidea are, in the majority, five pairs of branched, hollow appendages surrounding the peristome.

Surrounding the mouth are five teeth, supported by an elaborate system of ossicles (*Aristotle's lantern*, see p. 707), and a ring of processes, the *auricles*, from the interior of the corona, surrounds this and gives attachment to some of the muscles by which the ossicles are moved.

In the heart-shaped forms or Heart-urchins (Fig. 727) the corona is heart-shaped, the mouth is usually more or less eccentrically placed on the oral surface, and the peristome is usually transversely elongated; the anus is on or near the border between the two surfaces. The ambulacral areas do not run continuously, but stop short at the margin (*petaloid ambulacra*); one of them, the anterior, is usually unlike the others and frequently devoid of pores. The genital and ocular plates are in the middle of the aboral surface, where the ambulacra converge, and are thus widely separated from the anus; there are usually only four genital plates, and genital apertures may be reduced to two. Slender spines beset the entire surface and are the sole or chief organs of locomotion. Modified (ciliated) spines, the *clavulæ*, arranged in narrow bands or *fascioles*, are variously distributed round the anus and elsewhere, but are sometimes entirely absent. A few pedicellariæ are present in the neighbourhood of the mouth, and sphæridia also occur. The "lantern of Aristotle," with its teeth, is not represented.

FIG. 728.—**Clypeaster subdepressus,** view of aboral surface showing the petaloid ambulacra. (From Hertwig's *Lehrbuch*.)

In the Clypeastridea or Cake-urchins the whole corona (Fig. 728) is usually greatly compressed so as to assume the form of a disc, sometimes notched at the edges or pierced by fenestræ. The mouth is in the middle of the flat or concave oral surface, the anus eccentrically situated near the margin. The ambulacra are petaloid. The plates of the apical system are situated about the centre of the aboral surface, sometimes surrounding a centro-dorsal plate; sometimes more or less fused together. The spines are exceedingly fine and hair-like, those of the dorsal surface ciliated. Sphæridia and pedicellariæ are usually present, but clavulæ are absent. The dorsal podia are flattened and respiratory. An "Aristotle's lantern" with teeth is present, as in the globular forms, but often much simplified.

In the **Holothuroidea** the body is more or less elongated in the direction of the axis joining mouth with anus, which are placed at opposite (*anterior* or *oral*, and *posterior aboral* or *anal*) extremities of the body. The shape is sometimes completely cylindrical, sometimes five-sided; in many there is more or less dorso-ventral compression, and the dorsal and ventral surfaces may differ greatly from one another. A flattened sole-like ventral surface bearing the

three rows of tube-feet of the trivium is, as already stated, often distinguishable: it is most distinctly developed in *Psolus* and allied genera. In some Holothuroids the surface is enclosed in an armour of close-fitting plates; but in the vast majority the body-wall is comparatively soft, being strengthened merely by a great number of minute ossicles of a variety of shapes. In *Synapta* numerous minute anchor-like spicules, each connected with a latticed plate, project from the surface, and cause the animal to adhere to soft bodies with which it comes in contact. In the pelagic *Pelagothuria* and in *Rhabdomolgus*, as already mentioned, there are no hard parts of any kind. Around the mouth is a whorl of *tentacles*—pinnate, shield-shaped, or arborescent. The tube-feet are sometimes entirely absent. The arborescent tentacles are withdrawn by means of *retractor muscles*; withdrawal of the shield-shaped tentacles, however, is usually brought about by the action of *tentacle-ampullæ*; either mechanism of withdrawal is found in pinnate tentacles. When present they are usually uniform in character throughout, and may be arranged in five regular longitudinal rows, or scattered over the entire surface. Sometimes, as has already been stated in the account of Colochirus, the tube-feet of the dorsal and even some of those of the ventral surface may assume the form of papillæ. In the Elasipoda the tube-feet of the dorsal surface are remarkably modified, taking the form of greatly elongated processes.

In the **Crinoidea** the general shape is that which has been described in the case of the Feather-star—star-like, with a *central disc* and a series of radiating *arms*, which usually branch dichotomously. In the stalked forms (Fig. 729) a *stalk*, consisting of a row of elongated ossicles connected together by bundles of ligamentous fibres, attaches the animal to the sea-bottom. Along some of the joints of the stalk are usually arranged a number of slender, many-jointed appendages—the *cirri*. At its base the stalk usually breaks up into a number of root-like processes; distally it becomes continuous with the central disc. The ossicles forming the skeleton of the central disc are the *basals* and the *radials*: with the latter articulate externally the *brachials*, a single row of which gives support to each of the arms and its branches, while similar rows of smaller ossicles support the pinnules—the lateral appendages which fringe the arms in a double row. In the free forms the stalk is absent in the adult condition, though present on the larva, and from its terminal ossicle and other neighbouring plates is formed by coalescence a plate—the *centro-dorsal ossicle* of the disc. To the centro-dorsal ossicle are attached whorls of many-jointed, slender, curved *cirri*.

The mouth in all the Crinoidea, with one exception (*Comatula* (*Actinometra*)), is situated in the centre of the oral (upper) surface, and the anus in all, with the same exception, is eccentric and inter-radial. Running outwards from the mouth are a series of very narrow *ambulacral grooves*, one of which extends along the oral surface of each arm, giving off branches to the arm-branches and

to the pinnules. Bordering the ambulacral grooves and their branches are a pair of rows of short tubular *tentacles*, which correspond morphologically with the tube-feet of the other classes, but are devoid of the terminal suckers, and are not locomotory, but probably sensory and respiratory in function.

The **cœlome** in the Echinoderms is a wide cavity of enterocœlic origin lined by a ciliated cœlomic epithelium and containing a corpusculated fluid. Prolongations of it pass out into the rays, and, in the Ophiuroidea and Asteroidea, between the layers of the body-wall. In the Crinoidea it contains numerous strands of connective tissue. Special organs providing for respiration and excretion through the medium of this fluid are the *dermal branchiæ* or *papulæ* the *Stewart's organs*, and the *respiratory trees*. The first of these, which are confined to the Asteroidea and Echinoidea, have been described in the accounts of the Starfish and Sea-urchin. In most Asteroidea they occur only on the dorsal surface, but in some forms they are present on the ventral surface as well. In some of the Echinoids the place of dermal branchiæ in providing for the respiration of the compartment of the cœlome enclosing Aristotle's lantern (lantern-cœlome) is taken by *Stewarts' organs*, simple or arborescent bodies which project inwards from the peristome. The respiratory trees are referred to below in connection with the enteric canal.

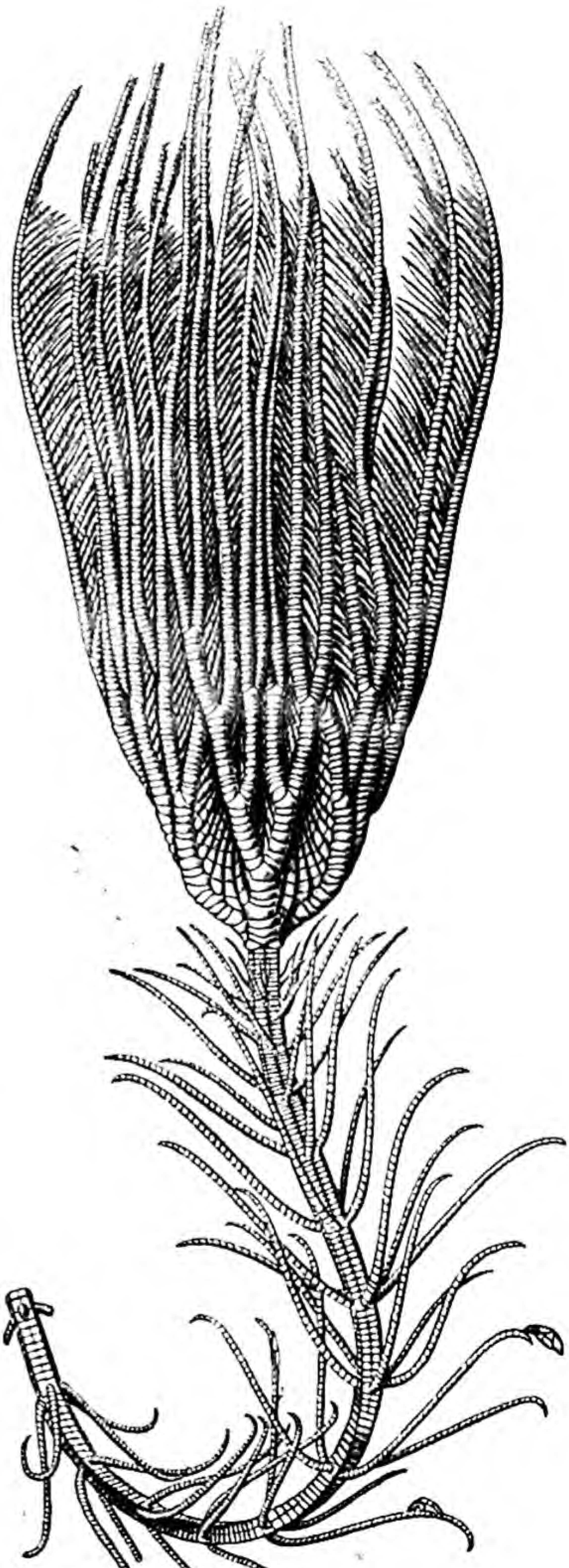


FIG. 729.—**Metacrinus interruptus.** (After P. H. Carpenter.)

Some reference has already been

made, in describing the general form of the body, to the **ambulacral system of vessels.** A ring-like *circum-oral* vessel (*ring-vessel*) in nearly all cases sends off a series of *radial* branches, one passing along each of the rays or ambulacral areas and giving off branches to the ampullæ of the tube-feet or to the tentacles. In most of the Holothuroidea branches pass forwards to the circlet of shield-shaped or branched oral tentacles, and in some cases there are vesicles or *ampullæ* at their bases. In the forms, in which tube-feet are wanting, radial vessels are also absent, and the vessels to the tentacles come off directly from the ring-vessel. In all the classes, except Crinoidea, one or more bladder-like appendages—the *Polian vesicles*—are in most cases connected with the ring-vessel. The *racemose vesicles*, or *Tiedemann's vesicles* (p. 695), are characteristic of the Asteroidea. In all, except the Crinoidea and the majority of the Holothuroidea, there is a communication between the ring-vessel and the surrounding water through the *madreporic canal*. In the Asteroidea, and in *Cidaris* among the Echinoidea, the wall of this tube is strengthened by numerous calcareous ossicles. In the Asteroidea, Ophiuroidea, and Echinoidea the communication with the exterior is through the madreporite. The fine pores perforating the madreporite and placing the madreporic canal in communication with the exterior, and the madreporic canal itself, are lined with strong cilia which move so as to drive a strong current inwards—the effect being to keep all parts of the ambulacral system in a condition of turgidity. In the few Holothuroids in which such a communication exists (*Elasipoda*) there is usually a simple opening, but sometimes a number of pores crowded together. In the remainder of the Holothuroidea the distal end of the madreporic canal or canals, lies free in the interior of the body-cavity, with which it is placed in communication by a number of perforations. In the Crinoidea there is no madreporic canal; but the ring-vessel is placed in communication with the cœlome by means of a system of ciliated *water-tubes*, while the cœlome communicates with the exterior through a number of minute *water-pores*, which perforate the oral body-wall. The fluid contained in the ambulacral system is similar to that in the cœlome, and contains similar corpuscles. In one Ophiuroid, however, the ambulacral system contains red corpuscles. Tiedemann's vesicles appear to have the function of manufacturing the corpuscles.

It cannot be definitely stated that a **blood-vascular system** exists in the Echinoderms. But two systems have been regarded as playing the part of blood-vessels—the *perihæmal* system and the *hæmal* system. Neither of these systems comprises vessels with contractile walls, and there is no definite circulation of the contained fluid. The perihæmal or, as it is sometimes termed, pseudohæmal system, is present in all the classes of the phylum. When typically developed (Asteroidea, Ophiuroidea) it consists of a ring-like circum-oral vessel or sinus and five radial vessels given off from it, together with an axial sinus and aboral ring-vessels. These " vessels " are channels with a

definite epithelial lining, and are of the nature of specialized parts of the cœlome, from which they are developed. In Asteroidea and Ophiuroidea the radial and ring-vessels, which lie between the corresponding parts of the ambulacral and epidermal nervous systems, are divided into two parts by a longitudinal septum, vertical in the radial, oblique in the ring-vessel. The axial sinus is nearly vertical in direction and partly encloses the axial organ in the way already described (p. 696). At its oral end it opens into the inner division of the circum-oral vessel: at its aboral end it opens into, or becomes closely applied to, the aboral vessel, which is in the form of a ring giving off radial branches towards the gonads: it may also communicate aborally with several of the pore-canals of the madreporite, and opens into the madreporic canal itself. In the Echinoidea the arrangement of the parts is modified in certain important respects. An oral ring-sinus is absent unless it be represented by the lantern-cœlome. The radial vessels of the system do not open orally into the lantern-cœlome: aborally they also terminate blindly, not opening into the aboral ring-sinus. The axial sinus is largely encroached upon by the axial organ: it terminates blindly at the oral end; aborally it communicates with the madreporic canal and is not connected with the aboral sinus. In the Holothuroidea there are five radial sinuses extending through the ambulacral areas between the superficial radial nerve and the radial ambulacral vessel, ending blindly aborally and opening orally into an oral ring-sinus. There is no axial sinus. In the Crinoidea the perihæmal system is greatly reduced, though representatives of the radial sinuses are present in the same situation as in the other classes.

The general disposition of the **lacunar** or so-called **hæmal system** in Asteroidea has been described in the account given of the structure of the Starfish (p. 690). Save for certain minor alterations which are involved in the change in the position of the madreporite, the system is arranged in the Ophiuroidea on the same plan as in the Asteroidea. In the Echinoidea there is an oral ring giving off five radial strands which in the greater part of their course occupy the typical position between the superficial radial nerve and the radial ambulacral vessel; aborally they terminate blindly. A gastro-intestinal system given off from the oral ring is highly developed, and there are an axial plexus in the axial organ and an aboral ring, with strands passing to the gonads, as in the Asteroidea. In the Holothuroidea there is an oral ring with radial strands, and a well-developed gastro-intestinal system. In the Crinoidea this system of lacunæ is highly developed and complicated in arrangement.

Whatever be its functions, this system is not a system of blood-vessels. It is made up of strands of a kind of gelatinous connective tissue, with many leucocytes, permeated in a very irregular way by minute lacunæ without definite walls. The great development of the gastric and intestinal branches of this system in some (Echinoids, Holothuroids) lends support to the view that its

main functions may be connected with the absorption and distribution of nourishment.

The **axial organ** (genital stolon) of the Echinodermata is closely connected both with the perihæmal and hæmal systems. Its general structure and relations in the Asteroidea have already been described (p. 696). In the Ophiuroidea there is a close correspondence with the Asteroidea, the chief differences being such as are involved in the change in the position of the madreporite from the aboral to the oral surface, and the resulting change in the direction of the madreporic canal and associated axial sinus and axial organ. In the Echinoidea the essentials are the same; but the axial organ has grown round the axial sinus so as to enclose it completely.

The **enteric canal** varies in the five classes more than any of the other systems of organs. It is a simple tube in the Holothurians and Echinoids, passing spirally through the body from the mouth at the oral pole to the anus at the opposite pole. In most of the latter group a complex masticatory apparatus with five teeth—the so-called "lantern of Aristotle"—is situated at its anterior extremity; the corresponding region in the Holothurians is surrounded by a circlet of ossicles, which protect the nervous and vascular rings and into which the longitudinal muscles of the body-wall are inserted.

In the Echinoidea there is a tubular cæcum, the *siphon*, connected with the intestine. In the Holothurians the so-called "respiratory trees" are branched appendages—usually two in number, sometimes single—of the cloaca or posterior wider portion of the intestine, and the "Cuvierian organs" are simple filiform glandular tubes, also connected with the cloaca.

The functions of the siphon and of the respiratory trees have already been referred to in the accounts of Echinus and Cucumaria. The Cuvierian organs, which occur only in a limited number of Holothurians, correspond to undivided basal branches of the respiratory trees: they are defensive organs, the animal when attacked throwing out numbers of these filaments, the secretion of which is very viscid and assumes the character of slender threads which may have the effect of entangling and hampering the assailant.

In the Crinoidea the alimentary canal is simply a coiled tube with both mouth and anal opening on the same (actual) surface of the body. In the Ophiuroids the central mouth leads into a simple sac giving off short diverticula, and there is no anal aperture. In the Asteroidea the alimentary canal is more complex than in the other classes. The stomach is divided, as already described in the account of the examples, into two portions, the cardiac and the pyloric, the former giving off five large rounded radial diverticula—the cardiac pouches or cardiac cæca, and the latter five pairs of very long branched diverticula—the pyloric or hepatic cæca. The intestine is short and conical and opens, in all but a few, by an anal aperture. In some Asteroidea (as in *Anthenea*, Figs. 695 and 697) the intestine has connected with it a system of

five elongated bifurcated inter-radial intestinal cæca; in others (as in *Asterias*, Fig. 693) these are represented only by two or three lobed diverticula. In one member of the class there are also ten cæca connected with the œsophagus.

In the **nervous system** of the Echinodermata three distinct parts, the relative development of which differs in the different classes, are to be recognized. These are the *epidermal* or *superficial*, the *deep*, and the *cœlomic* or *aboral*. The epidermal system is well developed in all the classes: its principal parts are a circum-oral nerve-ring and radial branches, but a plexus of nerve-fibres with occasional nerve-cells extends from it through the epidermis. In the Ophiuroids the radial nerves and the ring nerve are similar in their arrangement to what is to be observed in the Asteroids, but are more deeply placed, being covered over by the investing calcareous plates. The deep-lying nervous system is absent in the Crinoidea, very feebly developed in the Echinoidea, but well developed in the Asteroidea, Ophiuroidea, and Holothuroidea. Its general arrangement has already been described in the account of the Starfish. The aboral system is best developed in the Crinoidea and is absent altogether in the Holothuröidea.

The **sexes** are distinct in all the Echinoderms, with one or two exceptions; but there is very rarely any trace of sexual dimorphism. *Asterina gibbosa*, the Starfish, the development of which has been described (p. 698), is one of the exceptional hermaphrodite forms; the young animals of this species are male, producing sperms, but at a later stage they become female and produce only ova. In the family Synaptidæ of the Holothuroidea there are also numerous examples of hermaphroditism, the animal at first producing ova, later only sperms. In *Amphiura squamata*, an Ophiuroid, both ovaries and testes are present at once. The gonads, ovaries or testes as the case may be, are branching bodies, inter-radial in position, and usually in pairs. In the Asteroidea in general there are five pairs, the ducts from which open usually on a special plate on the aboral surface, but in one or two species on the oral surface. In *Pentaceros* and some other genera the gonads are more numerous. In the Echinoidea there are five ovaries or testes, the five ducts of which open on the genital plates of the apical system. In the Ophiuroidea there are ten pairs of gonads or groups of gonads, a pair in the walls of each of five pairs of *genital bursæ*, which open on the exterior by slits on the oral surface close to the mouth. In the Holothuroidea there is only a single branched gonad, sometimes imperfectly divided into two, with a duct opening on the dorsal surface not far from the mouth. In the Crinoidea the ovaries and testes occupy a remarkable position, being situated in the dilated bases of the pinnules; but, as in the other classes, they are connected by means of a *genital rachis* running through the arm with a centrally situated *genital stolon* (*axial organ*).

Development and Metamorphosis.—A few of the members of each class of Echinoderms are viviparous, in the sense that the development of the young

takes place in some sheltering cavity, or *brood-pouch*, on the surface of the body of the parent. But in most, development takes place externally, and the larvæ are free-swimming. The ovum in all undergoes regular and nearly equal cleavage, resulting in the formation of a ciliated blastula, which becomes invaginated so as to form a typical gastrula, like that of some Cœlenterata. The invaginated cells form the lining membrane (the endoderm layer) of an internal cavity—the primitive alimentary cavity or archenteron; the enclosing cells form the ectoderm; between the endoderm and ectoderm, and derived from the former, appear the cells of the mesoderm or middle layer. From the archenteron is given off a hollow outgrowth, the *enterocœle*, from which are derived the body-cavity with its enclosing peritoneal membrane, and the vessels of the ambulacral system with their various appendages. In the Crinoidea the vesicle destined to form the ambulacral system is developed independently of the cœlomic vesicles destined to form the body-cavity. A canal opening on the exterior by a dorsally situated opening, the *dorsal pore* (sometimes double), is formed by invagination from the surface ectoderm, and comes into relation with a canal arising as an outgrowth from the rudimentary ambulacral system to form the foundation of the madreporic canal of the adult. In the Crinoidea five dorsal pores and five canals finally are developed, but the two sets of structures do not enter into direct communication.

The part of the enterocœle (*hydrocœle*) destined to give rise to the ambulacral system, at first rounded, becomes compressed, and subsequently divided round the border into five lobes. Each of these lobes grows outwards to become developed subsequently into one of the five *radial ambulacral vessels* of the Echinoderm; the central part of the hydrocœle gives rise to the *ring-vessel* surrounding the œsophagus.

The cilia, which at first (in the gastrula stage) covered the surface of the larva uniformly, become restricted to a *peri-oral* band (Fig. 730, 1, 2 *por.*) surrounding a concave area on which the mouth opens. A smaller *adoral* band (1, 7, *aor.*) in the interior of the mouth has the function of attracting nutrient particles. The peri-oral band undergoes characteristic changes in the different classes, and the form of the larva at the same time becomes modified by the formation, except in the Crinoidea, of variously arranged processes along its course. The resulting larva, *echinopædium* or *dipleurula*, always exhibits marked bilateral symmetry. It has a pre-oral lobe on which an apical plate comparable to that of the trochophore may be developed.

In the Asteroidea the larva is either a *bipinnaria* (Fig. 730, 4 to 6) or a *brachiolaria*. The former has a series of bilaterally arranged processes or arms; the latter has, in addition, three processes not developed in the course of the ciliated band and used for fixation. The larva of Asterina, the development of which has been described and illustrated on pp. 698–704, is a greatly modified

bipinnaria with the pre-oral lobe large and eventually serving as a stalk, and the band of cilia confined to the edge of the larval organ and devoid of the

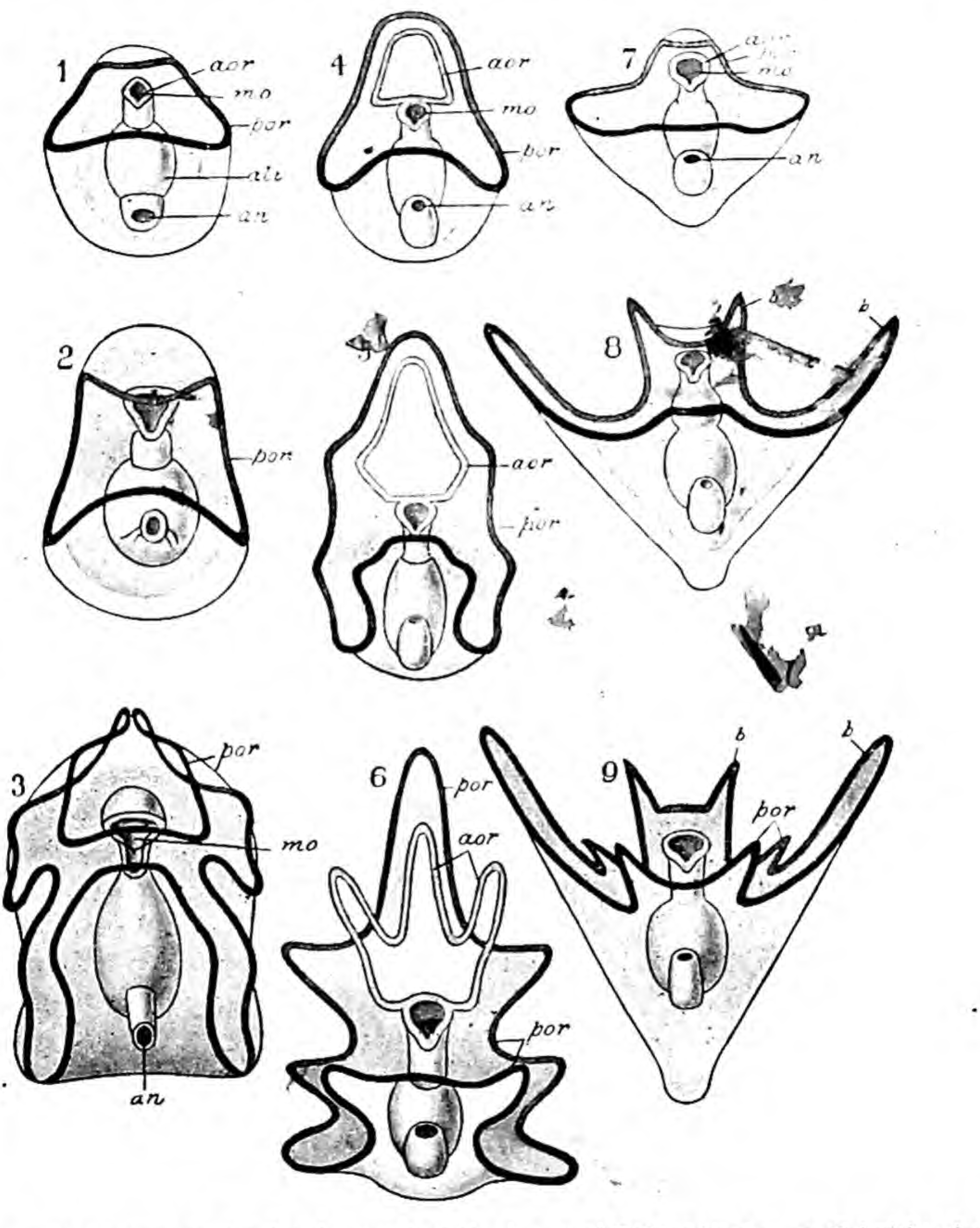


FIG. 730.—Diagrams of the development of the larvæ of **Echinoderms.** 1, Primitive form of Echinoderm larva; 2 and 3, Development of an *auricularia* (Holothuroidea); 4, 5, and 6, Development of a *bipinnaria* (Asteroidea); 7, 8, and 9, Development of a *pluteus* (Echinoidea and Ophiuroidea). *aor.* in 1 and 7, adoral band of cilia, in 4, 5, and 6, pre-oral loop; *ali.* alimentary canal; *an.* anus; *b, b.* processes or arms; *mo.* mouth; *por.* in 1, 2, 7, and 9, peri-oral ciliated band and processes, in 3, 4, 5, and 6, post-oral loop. (From Leuckart and Nitsche's Diagrams.)

bilateral processes of the normal bipinnaria. In at least one form the bipinnaria, developed in a brood-pouch, adheres to the parent by means of the

pre-oral lobe which takes the form of a short stalk. In general the bipinnaria is free-swimming and has a large pre-oral lobe the part of the ciliated band borne on which becomes separated off as a *pre-oral loop* (*aor.*) from the rest or *post-oral loop* (*por.*). In the course of both of these loops are the variously-arranged paired processes. In both the Ophiuroidea and the Echinoidea (Fig. 730, 7 to 9) the larva has the form which is known as the *pluteus*. The pluteus has a number of slender arms directed forwards and supported by a skeleton of delicate calcareous rods: the pre-oral lobe is reduced and the ciliated band is undivided. The larva of the Holothuroidea, the *auricularia* (2 and 3), has a number of short processes developed in the course of the ciliated bands; subsequently, in the *pupa* stage, the ciliated bands become broken up into a series of ciliated hoops encircling the body. Of the Crinoidea the development of *Antedon* alone is known. Blastula and gastrula stages occur as in the Starfish, but the history of the archenteron and its diverticula is widely different though the outcome is the same—viz., the differentiation of a primitive enteric canal, an anterior cœlome, from which a hydrocœle becomes separated off, and a pair of cœlomic sacs. The larva (Fig. 731) becomes barrel-shaped, and the pre-oral lobe, which is not very conspicuous, develops an ectoderma, thickening with a tuft of sensory cilia. The vibratile cilia on the surface are arranged in five transverse bands (*I—V*). Between the second and third of these is a wide shallow depression, the vestibule or stomodæum (1), which does not communicate with the mouth. After remaining in the free condition for a short time, the larva (Fig. 732) fixes itself by means of the pre-oral lobe, which elongates into a stalk, the cilia meanwhile being lost, and the apical plate absorbed. The vestibule becomes closed, and a solid rudiment of the adult œsophagus arises in close apposition with it. Round the œsophagus the hydrocœle grows in the form of a ring. The vestibule (*stom.*) with the œsophagus and hydrocœle are rotated so as to come to lie at the free extremity. The radial canals first appear as five tentacles which at first project into the cavity of the vestibule, and subsequently—when the latter opens out, as it soon does—on the exterior. The œsophagus (*œs.*), meanwhile, has become completed, and the mouth pierces the bottom of the now open vestibular cavity. The arms appear as five processes which soon

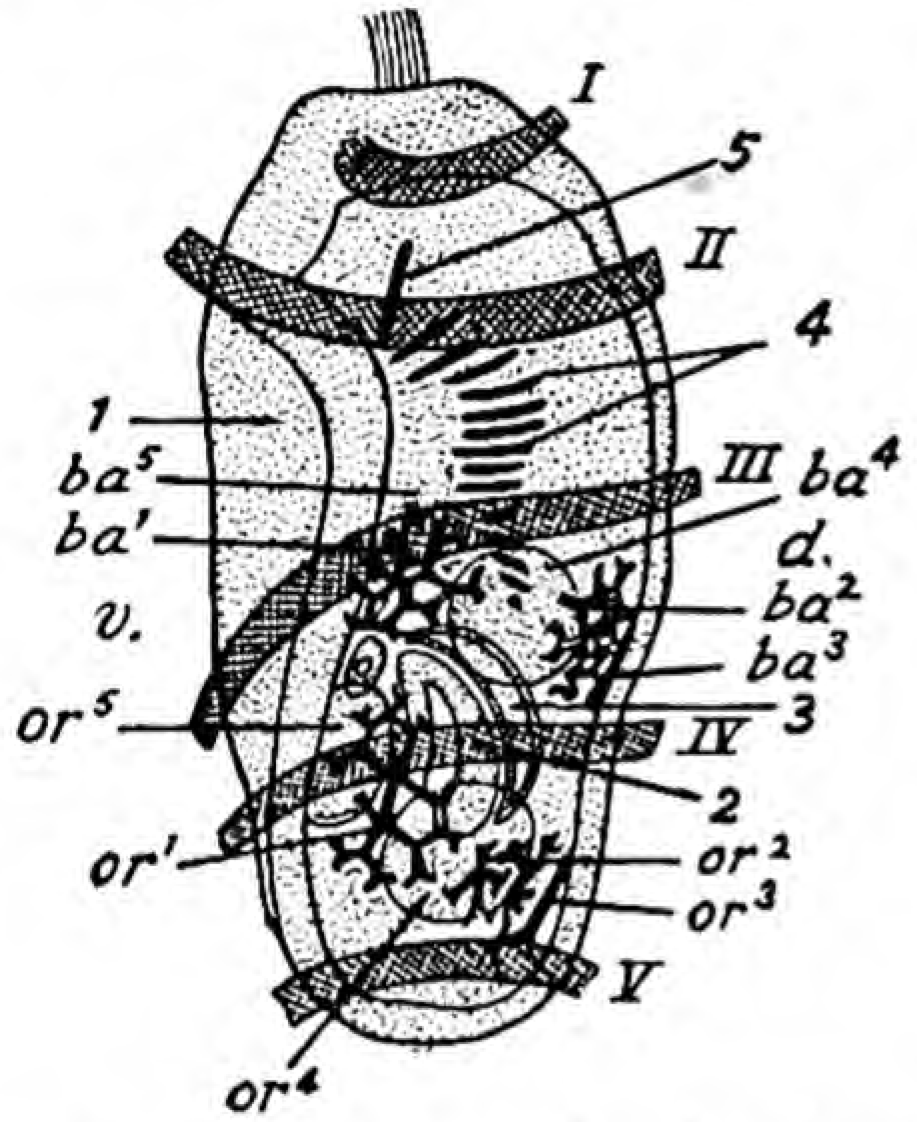


FIG. 731.—Free-swimming larva of **Antedon**, from the left side. *I—V*, ciliated bands; ba_1 to ba_5, the five basals; or_1 to or_5, orals; 1, vestibule; 2, intestinal vesicle; 3, right enterocœle; 4, calcareous joints of the stalk; 5, pedal plate. (From Lang, after Seeliger.)

bifurcate: the five radial canals become applied to them and undergo a corresponding division. The first plates are formed while the larva is still in the free condition; in the fixed condition they undergo further development, and extend into the arms as they grow. After about six months this *pentacrinoid* larva becomes free, by the absorption of the stalk and develops into the adult Antedon.

In the transition from the bilateral larva—pluteus, bipinnaria, brachiolaria, or auricularia—to the radial adult there is a marked *metamorphosis*. As the adult form is developed on one side of the larva, with its principal axis at right angles to that of the latter, the larval arms or processes become absorbed. In the Holothuroidea and Ophiuroidea all the organs of the larva are carried on into the adult; in the Asteroidea and Echinoidea the larval mouth and œsophagus are abolished and a new permanent mouth and œsophagus formed as a fresh invagination from the surface. In the very limited number of Echinoderms which are viviparous there is no such marked metamorphosis; but even in these the larva is at first distinctly bilateral in its symmetry.

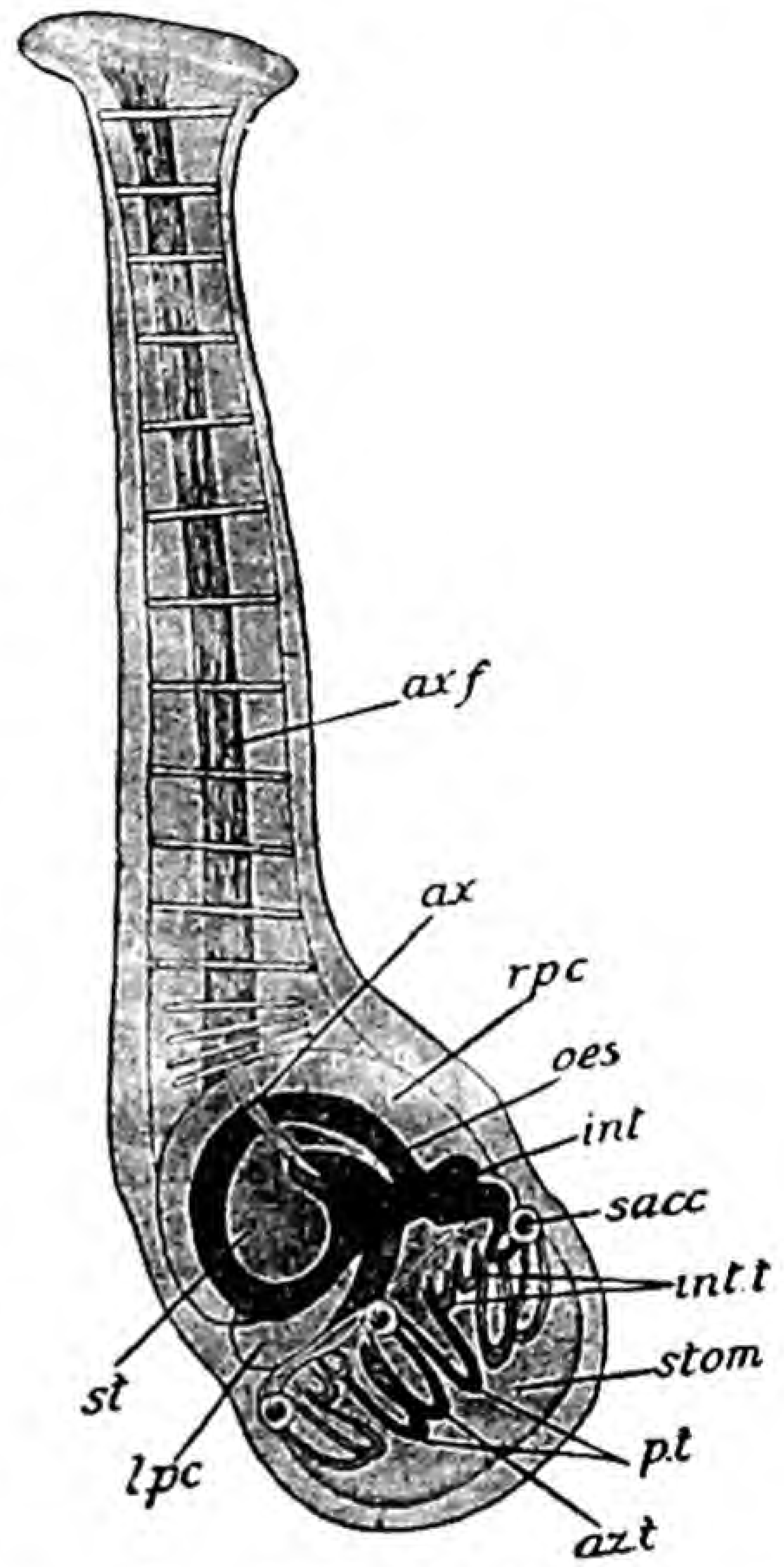


FIG. 732.—Fixed larva of **Antedon rosacea**, three and a half days after hatching, viewed from the side (decalcified). *ax.* axial organ containing the genital stolon; *ax. f.* axial band of fibres surrounding the chambered organ; *az. t.* azygous primary tentacle of the hydrocœle; *int.* rudiment of the intestine; *int. t.* inter-radial tentacles; *œs.* œsophagus; *p. t.* paired tentacles; *sacc.* rudiment of sacculus; *r. p. c.* right posterior cœlome; *st.* stomach; *stom.* larval stomodæum, now vestibule. (From MacBide's *Textbook of Embryology* (Macmillan & Co., Ltd.), after Seeliger.)

Modes of Life, etc.—The Echinodermata are without exception[1] inhabitants of the sea. In the adult condition the majority creep on the sea-shore or on the sea-bottom, the stalked Crinoids being exceptional in their permanently attached condition; but the larvæ of the great majority are *pelagic—i.e.*, live swimming in the upper strata of the ocean.

Echinoderms inhabit all depths of the sea, ranging from the shore between low and high water limits to the greatest depths. Members of all the classes are found at all depths; but the stalked Crinoids and the Elasipoda among the Holothuroidea are virtually confined to the deepest waters of the ocean, only one genus of the former and one species of the latter occurring in comparatively shallow water. Echinoderms are found in the seas of all parts of the globe.

[1] One species of Synapta is said to inhabit brackish water.

Like the majority of marine invertebrate groups, the phylum is more abundantly represented, as regards the number of genera and species as well as of individuals, in the warmer regions; the Crinoidea, the Holothuroidea and the Echinoidea are all much more abundant in tropical and warm temperate seas than in colder latitudes.

Echinoderms are of gregarious habits, large numbers of the same species frequently being found closely associated together in a comparatively narrow area. The movement of locomotion in the Starfishes is, as previously described (p. 688), a slow creeping one, through the agency of the tube-feet: the same holds good of the Echinoidea and those of the Holothuroidea that possess tube-feet. The footless Holothurians such as Synapta creep along with the help of the tentacles. Most of the Ophiuroids move by lateral flexions, sometimes sluggish, sometimes remarkably rapid, of the arms. The Comatulæ (Crinoidea), on the other hand, swim along by the flexion and extension of the pinnate arms propelling them through the water. Many Asteroids, Ophiuroids, and Echinoids bury themselves in sand or mud; others creep into narrow fissures in rock or coral. Movements of *manducation* are performed by the tentacles in the Holothurians: in the Starfishes the mouth papillæ are separated from one another and the cardiac part of the stomach is everted in order to enfold the prey, often of relatively large size. In those Echinoidea that possess a lantern of Aristotle there are very powerful and efficient movements of mastication. On the whole, as might be expected from the comparatively highly developed muscular and nervous systems, the co-ordination of movement is very much more complete in the Echinodermata than in the groups already dealt with.

A remarkable characteristic of the Echinoderms is the faculty of *self-mutilation* (*autotomy*) which many of them possess, together with the capacity for replacing parts lost in this way or by accidental injury. This is most marked in many Ophiuroids, some Asteroids, and some Holothurians, and does not occur at all among the Echinoids. Many Brittle-stars and some Starfishes, when removed from the water, or when molested in any way, break off portions of their arms piece by piece until, it may be, the whole of them are thrown off to the very bases, leaving the central disc entirely bereft of arms. A central disc thus partly or completely deprived of its arms is capable in many cases of developing a new set; and a separated arm is capable in some instances of developing a new disc and a completed series of arms. In some Starfishes (Ophiuroids and Asteroids) a process of separation of the arms and their development into complete individuals frequently occurs altogether independently of injury, and seems to be a regular mode of reproduction in these exceptional cases. Many Crinoids, also, readily part with their arms when touched and are able to renew them again; and some, at least, are capable of renewing the visceral sac of the central disc when it has become accidentally removed.

In the case of many Holothurians it is the internal organs, or rather portions of them, that are capable of being thrown off and replaced—the œsophagus or the cloaca with the Cuvierian organs, or the entire alimentary canal, being ejected from the body by strong contractions of the muscular fibres of the body-wall, and in some instances, at least, afterwards becoming completely renewed.

Three out of the eight classes of the phylum Echinodermata—the Cystoidea, Blastoidea, and Edriasteroidea—are represented only by fossil forms; and these are found only in rocks of the older (Palæozoic) formations, no representatives having survived to more recent times. Of the five classes that have living members, one, the Crinoidea, was very much more abundantly represented in the older geological periods than it is at the present day, the remains of stalked Crinoids forming great beds of limestone of Silurian to Carboniferous age: the free Comatulæ only appeared at a much later period. The other classes, or at least the Echinoidea, Asteroidea, and Ophiuroidea, were represented at a very early period by forms not very widely different from those now living; but the earliest Echinoids were peculiar in having the number of rows of plates variable, and in the plates overlapping one another. The Holothuròidea, owing to their comparatively soft integument, were less fitted to leave any remains in the form of fossils, yet Holothurian spicules have been found as far back as the Carboniferous.

Affinities.—The presence of radial symmetry was once regarded as involving a near relationship with the Cœlenterata, which were grouped with the Echinodermata under the comprehensive class-designation of *Radiata*. But on account of the presence of a bilateral symmetry underlying and partly concealed by the radial, we are led to the conclusion that whatever may have been the group of animals from which the Echinodermata were developed, there is every probability that it was a group with bilateral and not radial symmetry. The radial symmetry is evidently, as has already been pointed out, of a secondary character; it is only assumed at a comparatively late period of development, and even in the adult condition it does not completely disguise an underlying bilateral arrangement of the parts. Accordingly, within the phylum itself, it is reasonable to regard those classes as the more ancient which have the radial symmetry less completely developed. Again, the free condition which characterizes all existing Echinoderms, with the exception of a few Crinoids, is probably less primitive than the attached, since in other phyla the radial symmetry is co-ordinated with, and seems to be developed on account of, a fixed, usually stalked condition. Probably, then, stalked Echinoderms were the progenitors of the existing free forms, and these were preceded by primitive free forms with pronounced bilateral symmetry. It appears to be most probable that this ancestral form possessed the most essential features of the *dipleurula* larva (Fig. 733); *i.e.*, that it was a bilaterally

symmetrical form with a pre-oral lobe, simple alimentary canal with mouth on ventral surface and anus at posterior end; that it had a cœlome, originally developed from the archenteron of the gastrula; and that it had a band of strong cilia running around the concave ventral surface. Such a dipleurula-like form became converted, it is supposed, into a fixed form, such as that

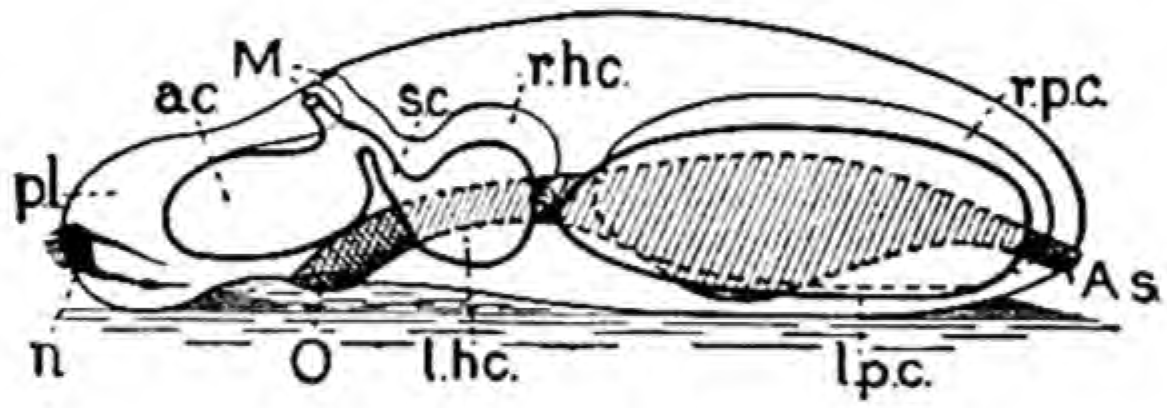


FIG. 733.—Reconstruction of the imagined **Dipleurula ancestor.** Anterior end on left of drawing; organs of left side towards observer, with stronger outline than those of right side. *As.* anus; *a. c.* anterior portion of cœlome; *l. h. c.* left hydrocœle; *l. p. c.* left posterior portion of cœlome; *M.* dorsal pore; *n.* nerve centre; *O.* mouth; *p. l.* pre-oral lobe; *r. h. c.* right hydrocœle; *r. p. c.* right posterior part of cœlome; *s. c.* connecting passage between the anterior portion of the cœlome and the hydrocœle. (From Lankester's *A Treatise on Zoology* (Adam & Charles Black, London.))

represented by some of the extinct class of the Cystoidea. The fixation must be supposed to have become effected through the medium of the pre-oral lobe, and further changes must have involved the shifting of the mouth to about the middle of the free surface. From this primitive Cystoid, thus regarded as the most primitive of all known Echinoderms, the remaining classes, both fixed and free, have been derived.

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